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FINAL REPORT

W-63-R(SI)-31

Ecology of white-tailed deer in Illinois

Submitted by
Cooperative Wildlife Research Laboratory, SIUC

Presented to
Illinois Department of Conservation

July 18, 1989

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FINAL REPORT

STATE OF ILLINOIS

W-63-R(SI)-31, STUDY IV

Project Period: July 1, 1986 through June 30, 1989

Study IV: Ecology of white-tailed deer in Illinois

Prepared by Alan Woolf and John L. Roseberry
Cooperative Wildlife Research Laboratory
Southern Illinois University at Carbondale

Need:

White-tailed deer management in Illinois has allowed increasing recreational use of the resource in response to an increasing deer population since the inception of the modern Firearms Season in 1957. Herd growth cannot be expected to continue, but demand for recreation will. Therefore, more precise management will be required to maintain or expand recreational benefits without jeopardizing herd welfare. General knowledge of deer behavior, biology, and ecology will not suffice; specific information on a herd or regional basis will be needed to implement sound management strategies.

Objective:

To determine the causes, timing, and rate of fawn mortality on the Union County Conservation Area and similar bottomland habitats; to determine the harvest statistics best suited to evaluate herd performance in Illinois; to determine taxonomic status of regional Illinois deer herds; and to determine causes of annual variation in condition indices and their suitability for monitoring herd status.

EXECUTIVE SUMMARY

This project began July 1, 1986 with 5 distinct Jobs. Job A (Fawn survival at Union County Conservation Area) represented a continuation from W-63-R(SI)-28; it was completed in Segment 29 and a Final Report provided in November 1987. Jobs B and D were completed this Segment; findings and recommendations are presented in this Final Report in accordance with requirements of Job E (Analysis and report). Only the abstract and recommendations for Job D (Temporal Variation in Condition Indices) are included in the body of this report; the entire final report for Job D is appended in the form of a thesis submitted in partial fulfillment of the requirements for a Master's degree in Zoology at SIUC.

Job C (Taxonomic status of regional Illinois deer herds) began in Segment 29 and will be concluded under a newly approved AFA. Preliminary results are presented as a portion of this Final Report.

JOB B. Harvest Statistics Evaluation

Objective: To determine the harvest statistics best suited to evaluate herd performance in Illinois.

INTRODUCTION

The recent proliferation of white-tailed deer (*Odocoileus virginianus*) coupled with their ability to exist in close proximity to human habitation has expanded the concerned public to include nonhunters and urban dwellers as well as hunters and rural landowners. This situation has created new challenges, opportunities, and problems for the deer manager. There is not, however, a consensus among professionals as to the type and amount of information necessary to manage the resource, nor the best means of utilizing available data. Hayne (1984), for example, believed that it was often sufficient merely to know a population's relative position with respect to carrying capacity and whether it was increasing or decreasing. McCullough (1979), on the other hand, argued that full utilization and precise objectives could be met only by knowing the actual number of deer present in a particular area. Many biologists contend that population modeling and simulation are essential for successful modern deer management (Gross 1972, Walters and Gross 1972, McCullough 1979, Burgoyne 1980, Pojar 1981). Hayne (1984), however, noted that continued biological monitoring of population indices was probably a more reliable means of determining population change than mathematically combining reproductive and mortality estimates (i.e., modeling). In some situations, data are insufficient to develop a model, and the manager must rely on other techniques out of necessity (Euler and Smith 1985). Even when modeling is possible, the prudent manager should periodically verify and validate the model with independent assessments of herd performance.

Annual hunter harvests are often the deer manager's primary source of information regarding the herd, and there are a variety of techniques and methodologies for the analysis of harvest data. These methods, which range from sophisticated mathematical treatments to simple intuitive interpretation, vary widely with respect to input requirements, output produced, and underlying assumptions. There is not general agreement as to which techniques are most applicable in given situations. In fact, there is a marked tendency for individual agencies to adopt and utilize a particular method (or variation thereof) to the exclusion of all others. Often, the accuracy and/or precision of these can only be assumed in the absence of verification with known data. Downing (1977:144) recognized this problem and suggested that: ". . . we need to look at a herd where we know what's happening in order to find out what data are most useful [for detecting what has happened or predicting what will happen]." In the opinion of Davis and Winstead (1980:244): "The failure of wildlife investigators to check population estimators against a known population is a deplorable situation."

Ideally, alternative methods of analysis should be tested and evaluated using a population of known composition and size, preferably one which has been dynamic rather than static. Unfortunately, such populations generally exist only on paper, or in very small, confined areas. An alternative would be to utilize a population that had been closely monitored over a long period of time using independent techniques and datasets. The white-tailed deer herd on Crab Orchard NWR (CONWR) in southern Illinois represents such a population. Since the late 1950's, this herd has been the focus of numerous studies and continuous monitoring by the Cooperative Wildlife Research Laboratory, Southern Illinois University. During that time, the herd has been alternately protected and hunted, and has undergone a period of growth, decline, and relative stability. Complete harvest data were collected during annual hunts from 1973 to the present. Annual abundance and trends were determined independently from a population model and from systematic roadside observations along a standardized 32-km census route.

Using the CONWR herd as the "standard", we tested and evaluated a number of herd monitoring techniques by comparing results with our retrospective knowledge of actual herd performance. We also applied selected techniques to regional Illinois deer herds for the period 1963-1988. We attempted to include representative techniques from all major categories of methods which utilize primarily harvest data.

The objective of this project was to develop practical guidelines for the deer manager to select the most appropriate herd monitoring technique using available harvest data. We compared such attributes as accuracy, precision, sensitivity, robustness, and data requirements. Mathematical and/or theoretical considerations were not emphasized; rather, we took a practical, management-oriented approach with the aim of producing a "handbook" for deer managers to aid in selection of realistic and suitable herd monitoring techniques given specific objectives and available data.

STUDY AREA

Crab Orchard National Wildlife Refuge (CONWR) is a 17,300-ha multiple use facility located primarily in Williamson County, southern Illinois. The refuge functions mainly as a wintering area for a large segment of the Mississippi Valley Canada goose (Branta canadensis) population. Other activities include a share-crop agriculture designed to provide food for wintering waterfowl, light industry, and recreation. The western portion of the refuge is open to public use. The eastern 7,300 terrestrial hectares, bisected into northern and southern halves by Crab Orchard Lake, is normally closed to the public and served as our principle study area. The area lies at the extreme southern edge of the Illinoian glacial till plain just north of the unglaciated Shawnee Hills Division of Illinois (Schwegman 1973). Most of the land is relatively flat to gently rolling and once supported small, relatively unproductive farms. The southwest and southeastern portions, however, are characterized by hilly, forested terrain. Current land use consists of a well-interspersed mix of 28% cropland, 9% pasture (mainly fescue; Festuca spp.), 11% oldfields in various successional stages, 46% second growth deciduous forest, and 6% pine plantations. Cropland primarily features row crops (corn, milo), red clover, and fallow on a rotational basis; about 1/4 of the row crops are left unharvested each year for wintering geese. Early oldfields are often dominated by broomsedge (Andropogon virginicus), fescue, and foxtail grasses (Setaria spp.). Intermediate oldfields general contain multiflora rose (Rosa multiflora), brambles (Rubus spp.), cedar (Juniperus virginiana), poison ivy (Toxicodendron radicans), and goldenrod (Solidago spp.). Later oldfields are usually sassafras (Sassafras albidum)-persimmon (Diospyros *virginiana*)-winged elm (*Ulmus alata*)-summac (*Rhus* spp.) associations, often followed by such species as sweetgum (*Liquidambar styraciflua*), shingle oak (*Quercus imbricaria*), and pin oak (*Q. palustris*). Many of the more mature, second growth woodlands are predominately oak-hickory, with stands of sugar maple (*Acer saccharum*) also common. Bottomland timber includes cottonwood-willow-sycamore (*Populus deltoides*, *Salix* spp., *Platanus occidentalis*) associations, mixed hardwoods, and pin oak flats. Pine plantations are mostly overstocked shortleaf (*Pinus echinata*) and loblolly (*P. taeda*) stands.

Soils are predominately Hosmer-Stoy-Weir silt loams on the uplands, Belknap-Sharon silt loams in the bottoms, and Wellston-Manitou silt loams on the unglaciated, forested slopes and ridges. The upland soils are moderately to poorly drained with slowly permeable subsoils. They are strongly acidic, and generally infertile and unproductive (Fehrenbacher and Odell 1959).

The southern Illinois climate is classified as humid continental. Daily and seasonal weather patterns are characteristically variable with generally hot, humid summers and cool to cold, damp winters. The average growing season is approximately 190-200 days. During our 16-year study, maximum daily temperatures in July (the hottest month) averaged 31.4 C while minimum daily temperatures in January (the coldest month) averaged -7.7C. Annual precipitation varied from 83.1 to 161.8 and averaged 118.6 cm. Most precipitation falls as rain, or rapidly melting snow. The average number of days per year with $\geq$ 15 cm of snow cover was < 7.

METHODS

Roadside Observations

In 1965, a permanent 32-km auto census route was established through representative habitat types on CONWR to monitor seasonal and annual changes in relative deer abundance and composition. Observations were conducted by 2 people from a slowly moving (32 kph vehicle) 1-2 hours before sunset; counts were not attempted during heavy rains and/or high winds. When possible, animals were classified as adult males, adult females, or fawns. Weekly counts were conducted 1966 through 1981. From 1982 to the present, counts were made twice weekly July through August, mid-September through mid-November, and January through February. Summer counts were for the purpose of estimating adult sex ratios, fall counts for determining prehunt abundance and fawn:doe ratios, and winter counts for determining posthunt abundance.

Harvest Data Collection

Controlled deer harvests on CONWR were held in conjunction with the Illinois firearm deer hunting season which consists of 2 3-day weekends about 3 weeks apart each autumn.. Hunting permits for CONWR were issued by lottery on a quota system. Successful applicants were allowed to hunt during 1 of the 2 3-day periods and harvest 1 deer of any sex or age by shotgun or muzzle loading rifle. Permittees were required to report to a central location prior to the hunt thereby ensuring an accurate count of the number of participants each year. Successful hunters were required to bring their deer to a designated check station; compliance was thought to be near 100%. At the check station, SIU personnel recorded sex, age, and dressed body weight of each animal, and antler beam diameter and number of points for bucks. Age was determined by tooth replacement and wear (Severinghaus 1949), primarily from jaws examined *in situ* by experienced biologists. Successful hunters were interviewed to determine location of kill, hours afield, and number of deer seen. Additional research information and/or materials were collected periodically.

Modeling

A deterministic computer model of the CONWR deer herd (Roseberry and Woolf 1983) was developed to 1) structure and assimilate existing knowledge about the herd; 2) aid in population analysis; and 3) facilitate management through simulation and prediction. For present purposes, the model was used to: 1) provide population estimates and trends for use in comparative evaluation of various analytical techniques; and 2) perform simulations to determine the effects of certain assumption violations.

Most big game models, including ours, are driven by 3 primary sets of variables representing harvest, reproduction, and natural mortality, with the latter being the least reliable. Our model's reproductive rates were based on conception and fetal rate data from over 870 does from CONWR (Crawford 1962, Roseberry and Klimstra 1970, and Unpubl. data, CWRL). Fawn survival from birth to 1st autumn was based on a 3-year telemetry study on CONWR (Nelson and Woolf 1987). Annual harvests were simulated by subtracting the actual recorded hunter harvests (plus estimated crippling and nonretrieval) from the model's current prehunt population for each of 10 sex/age classes. A range of natural mortality rates by sex/age class (excluding birth to autumn fawn mortality) were established based on field studies at CONWR (Hawkins et al. 1970, 1971) and elsewhere. Various combinations were then selected which were consistent with suspected herd growth from the early 1950's to the mid 1960's. The model was then "fine-tuned" (i.e., minor adjustments in mortality rates and density functions) until it conformed to observed trends (i.e. initial decline following early harvests then relative stability). It is important to note that once parameters and density functions were established, the model was not altered or "adjusted" each year to realign the population with roadside counts or harvest data. Two exceptions were that fawn mortality rates were increased during the model years 1977-78, 1978-79, and 1979-80 to conform to independently-observed adverse effects of 3 consecutive harsh winters, and fawn survival was increased during 1987 based on local and regional evidence of an exceptional fawn crop that year (above-normal fawn:doe ratios in counts and harvest and an unusually strong yearling class the following year). In addition, minor adjustments were made to crippling and non-retrieval rates as population density changed.

REFERENCE DEER HERD

White-tailed deer (4 does and 2 bucks) were released on what is now CONWR in 1942-43 by the Illinois Department of Conservation (Crawford 1962). By 1965, the protected herd had reached an estimated density of approximately 31/100 ha (Autry 1967). A special hunt was held in January 1966 which resulted in an estimated 65% herd reduction (Roseberry et al. 1969). The herd subsequently remained protected until 1973 when a series of annual hunts were begun that continued to the present. This section documents aspects of herd dynamics and vital statistics that form the basis for evaluation of alternative herd-monitoring techniques.

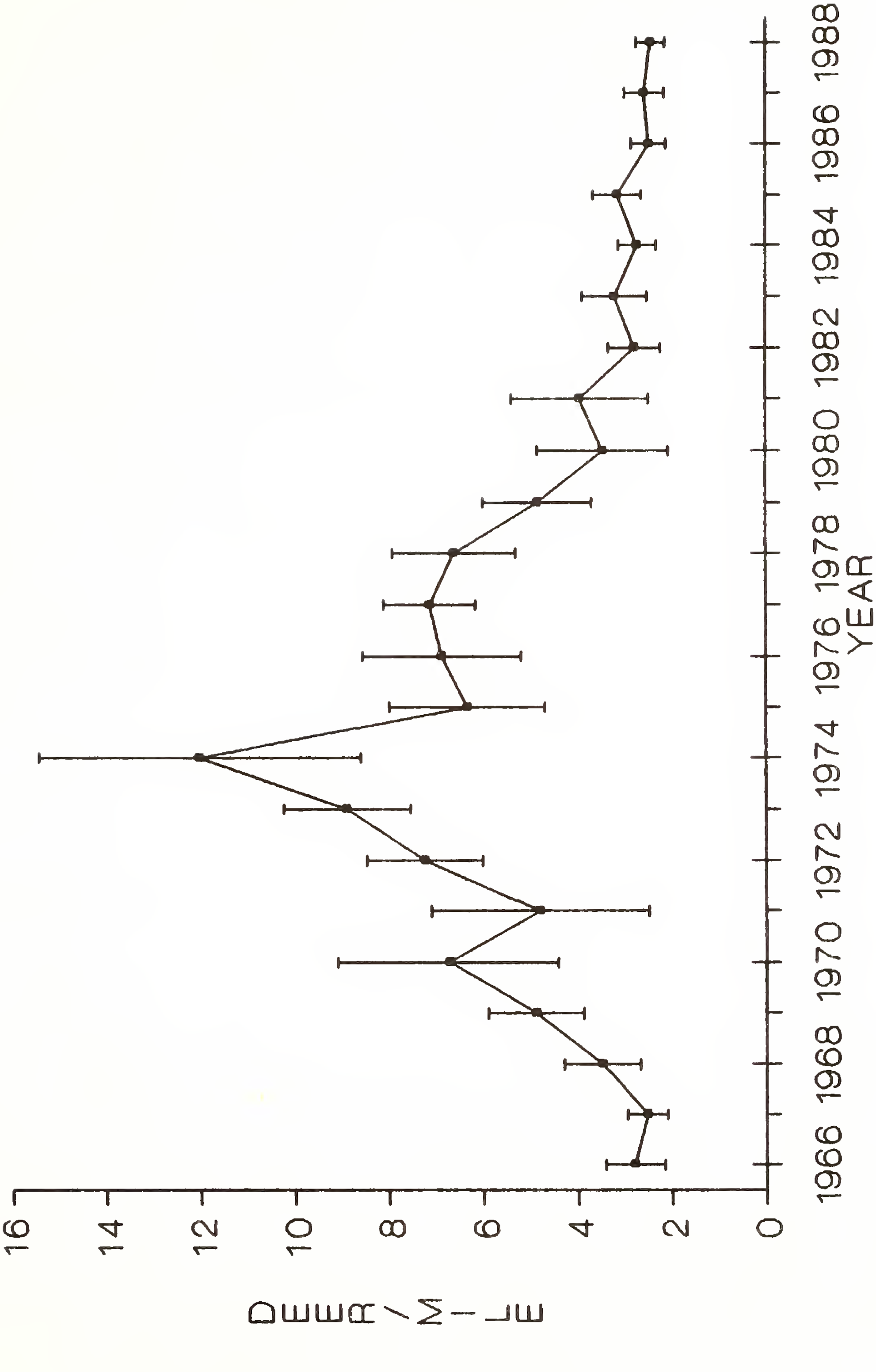
Hunter Harvests

During 1973 and 1974, permits were issued on a daily basis and hunt mechanics were not comparable with subsequent years. From 1975 through 1977, 600 permits were issued for the 1st season (south side only) and 200 for the 2nd season (north side only). From 1978 to the present, an equal number of permits have been issued for each season (total 900-1300) and permit holders have been allowed to hunt either side of the refuge (Appendix A). Annual harvests from 1973-1988 ranged from 451 to 1,115 (Appendix B). Overall, the sex/age breakdown was 54.3% males, 45.7% females; 29.3% fawns, 33.3% yearlings, and 45.7% adults.

Population Trends

Roadside observations.--Standardized roadside counts during September-November, expressed as deer seen/mile, were used as an index to annual changes in abundance on CONWR (Fig. 1). McCullough (1982) reported

Fig. 1. Mean number deer seen/mile and 90% confidence limits for weekly roadside counts, Crab Orchard NWR, September-November, 1966-1988.


DEER/MILE
0
2
4
6
8
10
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16
1966
1968
1970
1972
1974
1976
1978
1980
1982
1984
1986
1988
YEAR

that year-round weekly spotlight counts of white-tailed deer in Michigan were highest and least variable in October and November. Carbaugh et al. (1975) also recorded highest roadside spotlight counts in October and December. On CONWR, fall counts were less variable than winter counts (lower CV in 14 of 21 comparisons) but fewer deer were seen. Winter counts exceeded those of the previous fall in 5 of 6 years prior to hunting by an average factor of 1.45 (Appendix C). This differential is thought primarily due to differences in visibility associated with seasonal vegetational changes.

Deer seen/mile along the census route increased from a low of 2.52 following the initial hunt in 1966 to 15.03 in 1974. The latter figure is thought to be biased because more than 2 people participated in the counts; a more realistic estimate of 12.0/mile is hereafter assumed. Following initiation of annual harvests, the roadside index declined and stabilized at about 6-7 deer/mile for the next several years (1975-1978). Intensification of hunting pressure precipitated another decline (1979-1982) followed by a period of relative stability (1982-1988) at about 2.5-3.0 deer/mile (Fig. 1).

Modeling.--The simulated CONWR deer herd exhibited typical exponential growth from the early 1950's to 1966 when the 1st controlled harvest was conducted (Fig. 2). Following a temporary reduction, the herd again began rapid growth and achieved a maximum abundance of approximately 4800 animals in autumn 1973. Annual exploitation resulted in an approximate 25% decline over the next 2 years followed by a period of relative stability. Hunting effort was then intensified resulting in another 30% decline from 1978 to 1981. Since that time the simulated herd has been slowly declining; current

Fig. 2. Autumn population levels (from model) and hunter harvests, Crab Orchard NWR, 1950-1988.

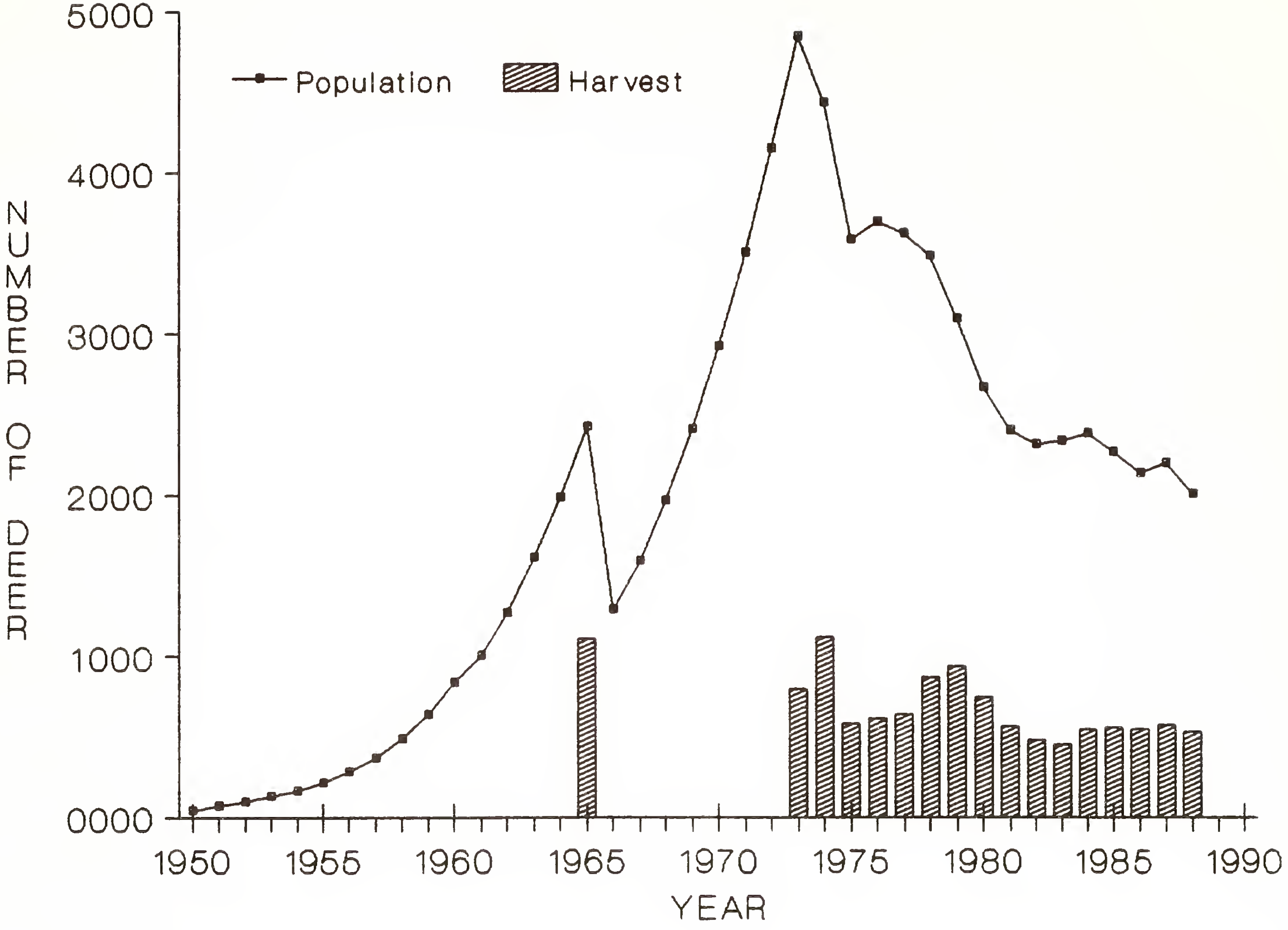
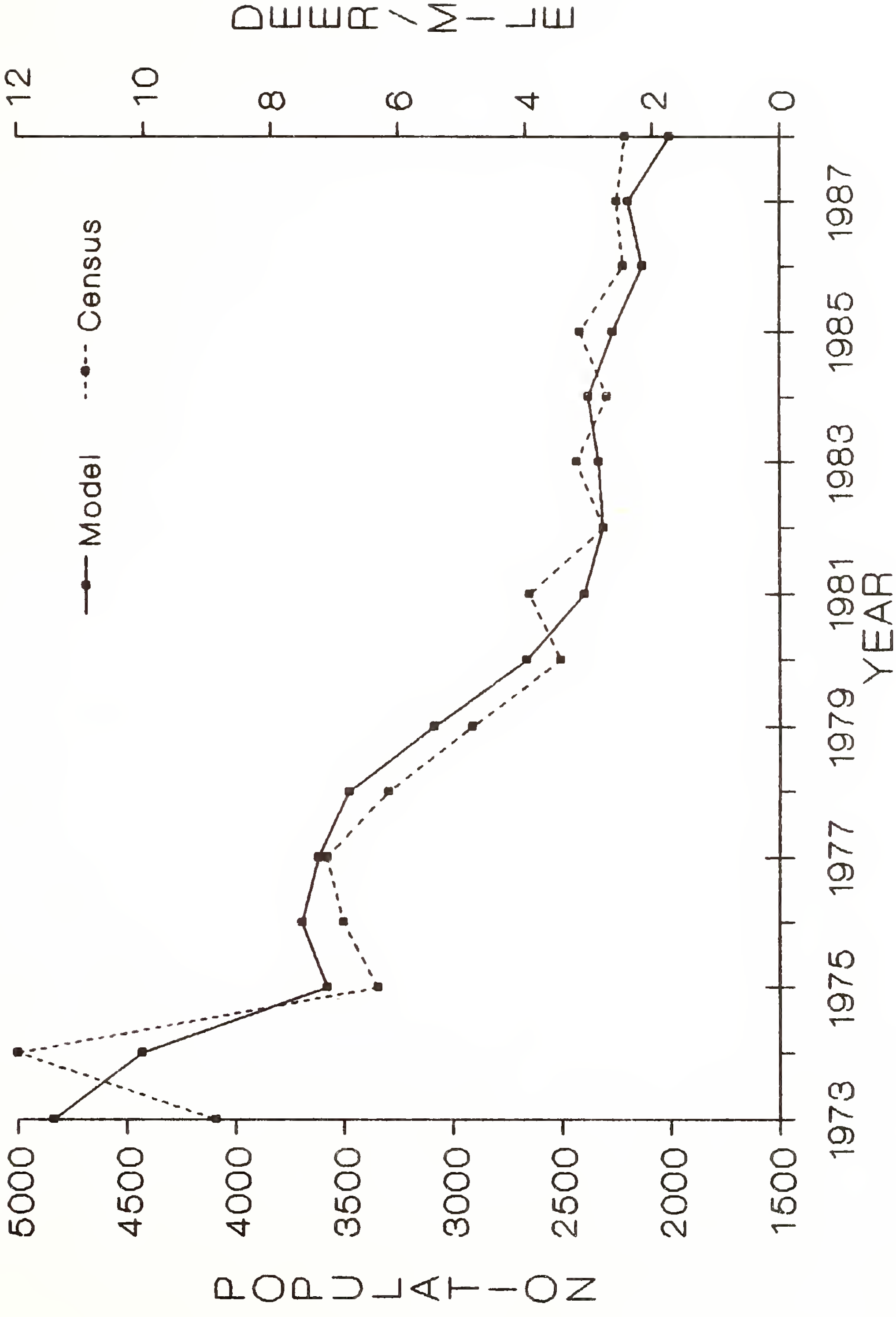

Population
Harvest
NUMBER OF DEER
5000
4000
3000
2000
1000
0000
1950
1955
1960
1965
1970
1975
1980
1985
1990
YEAR

Fig. 3. Population levels (from model) and corresponding roadside counts, Crab Orchard NWR, 1973-1988.


POPULATION
5000
4500
4000
3500
3000
2500
2000
1500
1973
1975
1977
1979
1981
1983
1985
1987
YEAR
DEER/MILE
12
10
8
6
4
2
0
Model
Census

estimated population size is 2000. Simulated population trends from 1973 to the present closely follow those indicated by the roadside counts (Fig. 3).

Vital Statistics

Several of the techniques evaluated use population statistics such as adult sex ratio and fawn:doe ratio in their calculations. Observational and harvest data from CONWR provided alternative methods of estimating these parameters as described below.

Adult sex ratio.--Adult sex ratio estimates were available from several sources including summer and fall roadside counts, modeling, harvest composition, reconstruction (Downing 1980), and relative representation of male and female yearlings in the harvests (Severinghaus and Maguire 1955). Computed adult sex ratios (males:100 females) ranged from 122:100 in the harvest to only 25:100 from fall roadside counts. Modeling, reconstruction, and the Severinghaus-Maguire method produced similar means of 53-56:100 (Table 1.). Annual estimates from the latter 2 methods were most highly correlated ($r = +0.88$; $P < 0.001$). Summer and fall estimates were only weakly correlated ($r = +0.57$; $P = 0.07$) with the former averaging 1.77 times more males:female than the latter. The harvest sex ratio was significantly correlated ($r = +0.66$; $P = 0.01$) only with the reconstruction estimate.

It was not unexpected that the highest adult male:female ratios were indicated by hunter harvests and the lowest by roadside observations. Roseberry and Woolf (1988) concluded from changes in daily and cumulative harvest structure that males were overrepresented in any-deer firearm seasons in Illinois; as they tend to be generally (Coe et al. 1980). In contrast, field observations almost always underestimate the relative abundance of males in the herd (Pojar 1979, McCullough 1982).

As noted above, similar mean adult sex ratios estimates were indicated by modeling, population reconstruction, and the Severinghaus-Maguire method. However, the model is not a valid estimator of this population statistic because output depended to some extent on arbitrarily selected sex-specific mortality rates. Similarly, the reconstructed sex ratio was influenced by arbitrarily selected lifetime harvest rates (0.70 and 0.55 for males and females, respectively). Theoretically, the Severinghaus-Maguire method should produce the most unbiased estimate if necessary assumptions are met. One of these assumptions is equal recruitment of the sexes into the yearling class. Several workers have utilized the sex ratio of the fawn harvest to "adjust" for a suspected preponderance of male recruitment into the yearling class (e.g. Creed et al. 1984). This is valid only if the fawn harvest is an unbiased estimate of the sex ratio in that cohort. However, male fawns are harvested at a higher rate than females (Coe et al. 1980, Roseberry and Woolf 1988). Therefore, use of fawn harvest data to "adjust" the yearling ratio would tend to bias M:F adult ratios upward. Use of this "adjustment" with the CONWR data produced M:F ratios 25% higher than those obtained without the adjustment. In actuality, the biased fawn harvest may make adjustment for unequal recruitment into the yearling class unnecessary. For example, if the prehunt sex ratio of fawns were 51:49 in favor of males, a 20% harvest at 55:45 would leave the posthunt population near 50:50. Another assumption of the Severinghaus-Maguire method is that male and female yearlings are equally susceptible to harvest. Roseberry and Woolf (1988), however, have shown that yearling males are the sex/age class most vulnerable to harvest. An overrepresentation of males in the yearling harvest would tend to bias the adult M:F ratio estimate downward.

Fawn:doe ratios.--Another key element of many population monitoring systems are fawn:doe ratios (usually used as a measure of recruitment). The CONWR data set provided an opportunity to compute and compare F:D ratios from a number of sources, including fall roadside counts, hunter harvests, reconstruction, and modeling (Table 2). Highest mean annual values came from reconstruction (1.21:1) and lowest from fall observations (0.66:1). Modeling and hunter harvests produced means of 0.91:1 and 0.94:1, respectively. Excluding the model, the most highly correlated annual estimates ($r = +0.80$; $P < 0.001$) were those of the harvest and reconstruction which, of course, were not independent. Noteworthy was the fact that the census F:D ratio was not correlated with the harvest ($P < 0.20$) and only weakly correlated ($r = +0.50$; $P = 0.05$) with reconstruction.

Based on previously described reproductive and fawn survival studies, autumn fawn:doe ratios on CONWR should approximate 0.92-0.94:1. Fall roadside observations of only 0.66 fawns per doe were clearly too low. Field studies by Downing et al. (1977) and McCullough (1982) have shown that fawns are less observable than does during all months in which the younger animals can be readily distinguished from yearling females (probably thru November or December). Reconstructed fawn:doe ratios, on the other hand, appear to be inflated. As seen in Table 2, reconstructed F:D ratios for any given year always exceeded the harvest ratio for that year. This discrepancy resulted because progeny/progenitor ratios increased with each age class. For example, ratios from the composite CONWR harvest for progeny classes 0.5 through 3.5 were 0.90, 1.53, 1.75, and 2.04. Thus, as successive years were added to the reconstruction, the F:D ratio progressively deviated (exceeded) from the initial harvest. Similar trends in other areas have been interpreted as an underrepresentation of fawns in the harvest (Eberhardt 1960). We do not believe this to be true on CONWR (Roseberry and Woolf 1988); rather, it appears that adult cohorts become progressively underrepresented in the harvest as they increase with age. At least 3 factors could contribute to this: 1) normal age-specific mortality patterns, 2) differential age-specific vulnerability to harvest, and 3) errors in age determination. Regarding the latter possibility, age determination of fawns and yearlings appeared to be satisfactory on CONWR, but there was some evidence that the 2.5 year age class was inflated due to underaging of 3.5 and possible 4.5-year-old animals (Roseberry 1980).

Whether or not harvest fawn:doe ratios are unbiased indicators of recruitment is a matter of debate (Coe et al. 1980). Eberhardt (1960) thought that fawns were underrepresented in Michigan harvests as did Murphy (1961) in Missouri. Others, however, believed them to be more vulnerable than older animals (Gill 1953, Van Etten 1965). Nixon (1970) reported that harvest fawn:doe ratios were representative in Iowa but too high in Ohio. As Maguire and Severinghaus (1954) noted, hunter selectivity is probably the most important determinant of fawn harvest. Furthermore, such selectivity could be expected to vary regionally according to traditions and hunter attitudes (Roseberry and Woolf 1988). In Illinois (and CONWR), there is perhaps less hunter bias against shooting fawns because any-deer seasons have been in effect since modern firearm hunting was begun in 1957. Roseberry and Woolf (1988) examined daily and cumulative changes in the Illinois deer harvest and concluded that fawns may have been underrepresented in the total harvest but not the antlerless harvest. Based on this finding, and the fact that harvest fawn:doe ratios on CONWR were very near those predicted by independently-obtained reproductive and fawn survival rates, we conclude that the harvest data is representative of actual herd composition with respect to these 2 age groups.

Table 1. Adult sex ratios (M:100F) from various sources, Crab Orchard NWR, 1973-1988.

Year	Census		Harvest		Recon-	
	Summer	Fall	Absolute	Calculated[a]	struction	Model
1973	56.6	29.9	150.0	89.1	78.2	72.2
1974	43.1	42.5	116.0	85.7	69.2	61.1
1975	59.6	40.5	148.3	59.1	66.7	51.9
1976	41.7	27.7	152.9	72.4	57.0	50.4
1977	46.6	22.3	161.5	62.3	51.4	47.6
1978	32.2	17.7	105.3	46.1	42.6	42.9
1979	35.8	19.8	87.3	44.3	43.2	40.5
1980	40.0	25.6	92.5	46.2	41.9	44.6
1981	--	17.2	93.0	45.2	44.4	50.1
1982	42.5	26.8	100.7	52.9	45.7	54.1
1983	--	22.3	124.1	50.0	52.8	57.7
1984	32.4	18.6	99.5	58.0	45.6	58.0
1985	59.4	25.3	96.7	43.3	46.6	59.7
1986	--	18.6	107.4	42.4	--	60.2
1987	--	24.0	155.2	43.5	--	61.4
1988	--	23.5	164.3	50.9	--	56.0
Mean	44.5	25.2	122.2	55.7	52.7	54.3
SD	10.0	7.4	28.2	14.9	11.8	8.2

[a] Severinghaus and Maguire (1955).

Table 2. Fawn:doe ratios from various sources, Crab Orchard NWR, 1973-1988.

Year	Census	Harvest	Reconstruction[a]	Model
1973	0.85	0.79	1.23	0.82
1974	0.87	0.76	1.14	0.80
1975	0.63	0.90	1.46	0.85
1976	0.61	1.04	1.33	0.87
1977	0.41	0.78	0.88	0.80
1978	0.59	0.82	0.98	0.83
1979	0.56	0.75	0.96	0.84
1980	0.69	0.87	1.13	0.93
1981	0.72	0.89	1.20	0.94
1982	0.72	1.08	1.39	0.93
1983	0.54	0.96	1.19	0.94
1984	0.64	0.79	1.07	0.93
1985	0.79	1.12	1.41	0.93
1986	0.61	1.05	1.23	0.96
1987	0.75	1.39	1.60	1.24
1988	0.61	1.06	1.21	0.90
Mean	0.66	0.94	1.21	0.91
SD	0.12	0.17	0.19	0.10

[a] Last 3 years based on estimate of q for individual cohorts (Fryxell et al. 1988)

EVALUATION OF TECHNIQUES

Technique I: Index-Removal

Description

Petrides (1949) described a method whereby the difference between an index of abundance before and after a known removal can be used to estimate population size prior to that removal.

Procedure

$$N = \frac{I_1 C}{I_1 - I_2} \qquad \text{where}$$

N = population size before removal

I_1 = index of density before removal

I_2 = index of density after removal

C = number of animals removed

Assumptions

1. Indices are linear estimates of density.
2. Removals have only a numerical effect on 2nd index (i.e., they do not alter vulnerability, behavior, etc).

Input

1. Index of density before and after hunting season.
2. Estimate of total harvest (+ crippling loss)

Output

1. Estimate of absolute prehunt population size.

Test Data

Fall and winter roadside counts were used as pre- and posthunt indices of abundance. Known harvest plus estimated crippling was used as removal. Winter counts were adjusted (x 1.45) to account for the fact that they typically exceeded fall counts in the absence of hunting. In addition, 3 indices of density obtained during 1st and 2nd hunts (sightings/hour, kill/hour, and hunter success) were tested using 1st season harvest plus estimated crippling as removal.

Results

Estimates based on fall and winter roadside counts produced one excessively large value (>12,000) with others ranging from ranging from 1099 to 3848. However, annual estimates were erratic and did not follow population trends. Estimates based on the 1st and 2nd season indices produced both negative and excessively large estimates and in general performed unsatisfactorily (Table 3).

Discussion

Theoretically, this method should provide a relatively easy way to estimated the abundance of harvested populations. Under actual conditions, however, the technique proved unsatisfactory. The apparent problem was a violation of the critical assumption that the difference between pre- and posthunt indices was due solely to the numerical removal of animals. The observability of various sex/age classes of white-tailed deer varies seasonally (Carbaugh et al. 1975, Downing et al. 1977, McCullough 1982) due to behavior, social organization, habitat conditions, weather, etc. On CONWR, winter (post) counts averaged 1.45 times higher than fall (pre) counts during the 6 years prior to harvesting thus suggesting that factors other than abundance were affecting observability. In addition, hunting-related changes in behavior and sex/age composition were also thought to have affected observability.

References

1. Petrides, 1949 (original)
2. Caughley, 1977 (descriptive)
3. Eberhardt, 1982 (descriptive)

Table 3. Index-removal population estimates, Crab Orchard NWR, 1973-1988.

Year	Index of Abundance[a]				
	1	2	3	4	5
1973	--	--	--	--	3848
1974	--	--	--	--	2480
1975	--	--	--	--	12187
1976	--	--	--	--	3833
1977	--	--	--	--	2126
1978	1391	1282	3349	**	2315
1979	3066	2139	2952	5193	2081
1980	1764	1760	**	4844	1434
1981	2024	1100	**	1689	1207
1982	1919	1663	11780	3023	2339
1983	1948	948	10583	1446	3361
1984	13923	1754	**	2651	1680
1985	**	11698	**	8679	1099
1986	5550	1744	**	2457	1732
1987	1420	847	1737	1316	2056
1988	2305	2922	3531	6986	--

[a] 1 Kill/hour for successful hunters.
2 Kill/hour for all hunters (unsuccessful X 15).
3 Sightings/hour for successful hunters.
4 Percent hunter success.
5 Pre- and posthunt (adjusted) roadside censuses.
-- Seasonal hunts prior to 1978 were held on separate parts of the area.
** Negative estimate.

Technique II: Catch Per Unit Effort

This group of methods is based on the assumption that the ratio of animals "caught" to effort expended is proportional to the number of animals in the population at the beginning of the capture period. "Catch" can be defined in a number of ways such as animals harvested or seen while "effort" can be measured as hours hunted, hunters afield, permits issued, etc.

Variation A: 2-Catch Method

Description

When 2 catches are taken with equal effort, population size prior to the first catch can be estimated as:

$N = C_1^2/(C_1-C_2)$ where

C_1 = 1st catch

C_2 = 2nd catch

N = population size prior to 1st catch

Assumptions

1. Probability of capture is constant for all animals for each sampling period.
2. Population is "closed" between harvesting periods (i.e., no births, deaths, ingress, or egress).

Input

1. Harvest and effort data for 2 periods of equal effort.

Output

1. Estimate of absolute population size.

Test Data

1st and 2nd season harvests, 1978-1988.

Results

Annual estimates varied from 1162 to 8571 with no apparent tendency to track population trends.

Discussion

This particular method did not perform satisfactorily, probably due to differential vulnerability between seasons related to weather, behavior, etc. This is essentially the same problem encountered with the Index-Removal method (Technique I).

References

1. Zippin, 1956 (original)
2. Seber and LeCren, 1967 (descriptive)
3. Caughley, 1977 (descriptive)

Variation B: Leslie Method

Description

This method, first developed by Leslie and Davis (1939), is described by Caughley (1977:44): ". . . catch per unit of effort plotted against [the] previous cumulative catch provides a straight line cutting the x-axis at the population size prior to harvesting." Therefore:

$Y = a - bX$; and $N = -a/b$; where

Y = catch/unit effort

X = cumulative catch

N = preharvest population size

a and b = coefficients from regression equation

Assumptions

1. Probability of capture is constant for all animals for each harvesting period.
2. Population is closed between harvesting periods.
3. Each unit of effort takes a constant proportion of the remaining population.

Input

1. Estimates of catch/unit effort and cumulative harvest for at least 2 periods.

Output

1. Estimate of absolute population size.

Test Data

Kill/hour for all hunters and percent hunter success was plotted against cumulative kill for each day of the 10-day CONWR hunt conducted January 1966 (Roseberry et al. 1969). Daily data from annual hunts could not be used because effort was recorded by season only. Kill/hour, sightings/hour, and hunter success during 1st and 2nd 1978-1988 seasons were used in 2-pt regressions with cumulative harvest.

Results

Results from the 10-day 1966 CONWR hunt are shown in Figure 4. The kill/hour data indicated a prehunt population of 1,554 while the hunter success date produced an estimate of 1,788. These estimates are about 20-30% below expected.

The 2-pt regressions using 1978-1988 seasonal data produced results essentially identical to those of the Index-Removal method described previously.

Discussion

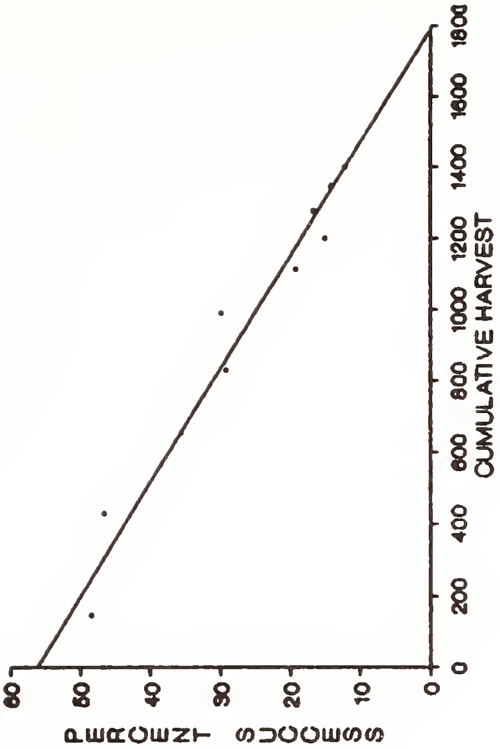
For the above technique to be successful, catchability must remain constant throughout the season. Working with the same 1966 CONWR data set, Roseberry and Klimstra (1974) concluded that vulnerability was not constant over time, but declined slightly as the season progressed due to behavioral changes and shifts in sex/age structure of the remaining herd. Eberhardt (1960, 1982) agreed for deer and sporthunting generally. If "catchability" does decline seasonally, a straight-line fit of the data points would underestimate actual population size (Lewis and Farrar 1968) In fact, visual inspection of the CONWR data points suggests that a better fit could be achieved by a slightly curved line which would also produce a higher population estimate. Conner et al. (1986), however, reported that the technique produced "reasonably accurate" results when compared with 2 independent estimates of deer abundance at Remington Farms, Maryland.

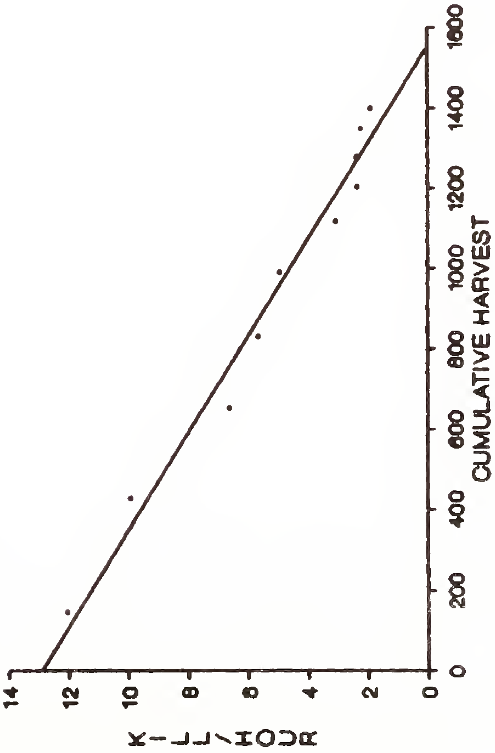
Reasons for failure of the 2-pt regressions using 1978-1988 seasonal data were the same as described for the Index-Removal Method utilizing the same data.

References

1. Leslie and Davis, 1939 (original)
2. Eberhardt, 1960 (descriptive)
3. Caughley, 1977 (descriptive)
4. Seber, 1982 (descriptive)
5. Lewis and Farrar, 1968 (application)
6. Conner et al., 1986 (application)

Fig. 4. Daily kill/hour and percent hunter success vs cumulative harvest, Crab Orchard NWR, 1966.


PERCENT SUCCESS
60
50
40
30
20
10
0
0
200
400
600
800
1000
1200
1400
1600
1800
CUMULATIVE HARVEST


KILL/HOUR
14
12
10
8
6
4
2
0
0
200
400
600
800
1000
1200
1400
1600
CUMULATIVE HARVEST

Variation C: Direct Index

Description

This approach is based on the premise that catch/unit effort is a function of population size and can therefore serve as an index to the latter.

Assumptions

1. Catch/unit effort is a linear function of population size.

Input

1. Some measure of effort expended and success achieved.

Output

1. An index of population size.

Test Data

Annual estimates of deer abundance on CONWR were compared with 4 indices of catch/unit effort: 1) sightings/hour, 2) kill/hour for successful hunters, 3) kill/hour for all hunters, and 4) percent hunter success (Table 4, Fig. 4). The number of hours for all hunters was estimated by assuming that unsuccessful hunters spent an average 15 hours afield.

Results

All indices of catch/unit effort were significantly correlated with estimated population size ($P < 0.01$). The index most strongly and linearly related was percent hunter success ($r = +0.98$) followed by sightings/hour ($r = +0.97$), kill/hour for all hunters ($r = +0.96$), and kill/hour for successful hunters ($r = +0.80$).

Discussion

Several studies have reported linear relationships between population size and kill/hour on a daily (Van Etten et al. 1965, Holsworth 1973, Grau and Grau 1980) and annual (Van Etten et al. 1965) basis. Our data exhibited similar trends, although there appeared to be a slight tendency for the kill/hour lines to flatten out at the lower densities (Fig. 5). As an indication of this, log transformations of both kill/hour indices produced slightly better fits with corresponding population size. It is also noteworthy that even though the index for all hunters required an arbitrary estimate of the time spent afield by each unsuccessful hunter, it was still preferable to using only successful hunters to measure kill/effort.

Similar to the kill/hour indices, the relationship between population size and sightings/hour appeared to be slightly curvilinear (Fig. 5). Roseberry and Klimstra (1974) noted a similar trend during a 10-day hunt on CONWR in 1966. Nevertheless, the data generally support Downing et al's (1965) contention that hunter observations per unit time could be used to indicate year to year population trends on the same area.

As noted above, the strongest and most linear fit with annual population size was obtained by using percent hunter success (total kill/total hunters) as the catch/unit effort index. This is fortuitous in that this index is also the easiest and least expensive to obtain. Hansen et al (1986:375) reported that: "No daily weather conditions or combinations thereof appeared to consistently affect the annual [statewide Illinois] harvest of deer." This appeared to be true on CONWR too as virtually all of the annual variation in hunter success could be explained by prehunt deer abundance. Freddy (1982) reported a similarly strong correlation for mule deer (*O. hemionus*) in Colorado.

References

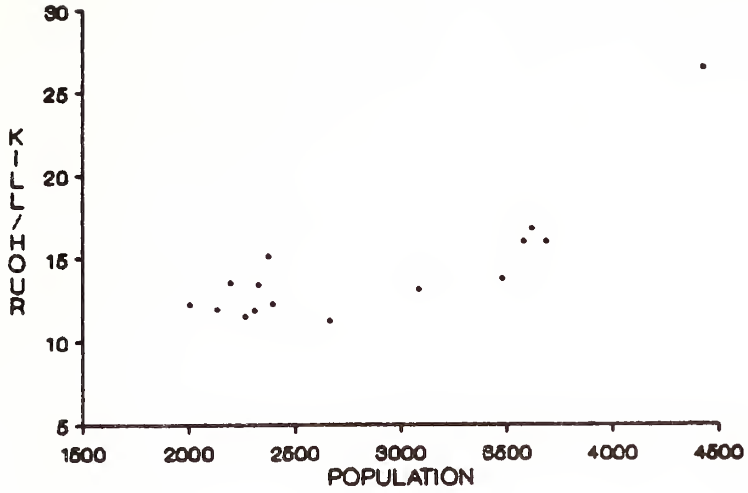
1. Eberhardt, 1960 (descriptive)
2. Downing et al., 1965 (application)
3. Van Etten et al., 1965 (application)
4. Holsworth, 1973 (application)
5. Roseberry and Klimstra, 1974 (application)
6. Grau and Grau, 1980 (application)
7. Freddy, 1982 (application)

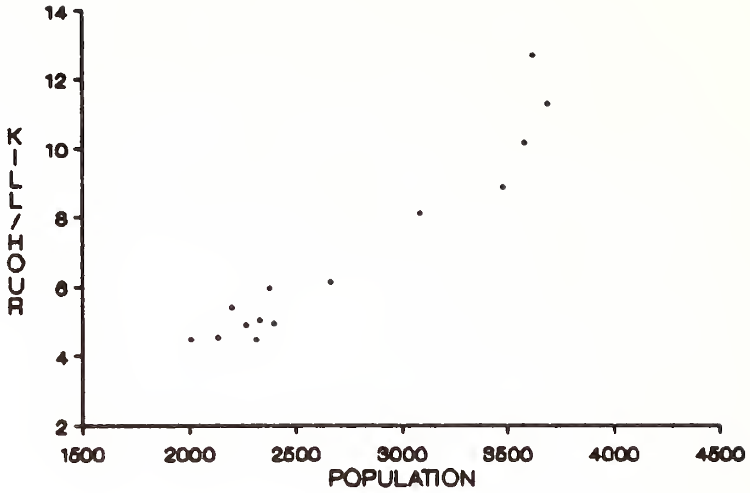
Table 4. Indices of catch/unit effort vs population size, Crab Orchard NWR, 1974-1988.

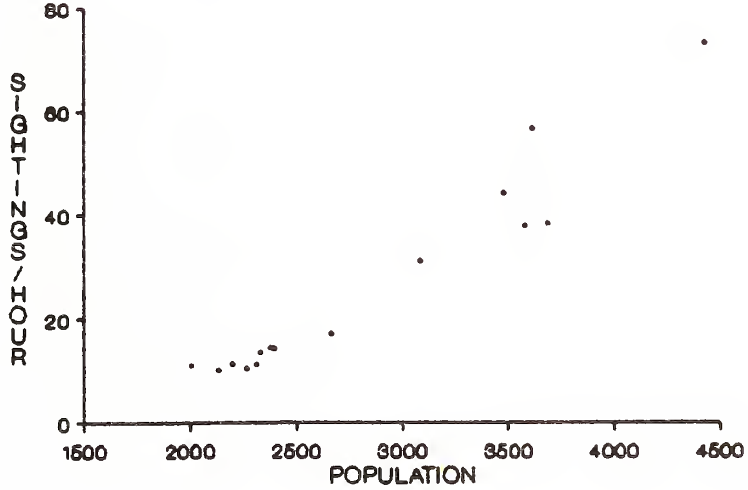
Year	Population Size	Catch/Unit Effort Index[a] 1	2	3	4
1974	4429	26.41	**	73.13	**
1975	3578	16.02	10.15	37.89	80.61
1976	3690	16.02	11.31	38.30	85.24
1977	3616	16.72	12.67	56.58	88.69
1978	3475	13.76	8.86	44.12	78.85
1979	3084	13.10	8.13	31.19	76.27
1980	2661	11.23	6.14	17.15	67.00
1981	2394	12.30	4.93	14.29	55.26
1982	2310	11.92	4.48	11.23	51.84
1983	2328	13.39	5.03	13.51	54.73
1984	2375	15.12	5.98	14.44	59.74
1985	2263	11.53	4.89	10.39	56.05
1986	2130	11.91	4.53	10.15	52.35
1987	2194	13.49	5.40	11.34	57.49
1988	2003	12.26	4.47	11.04	51.31

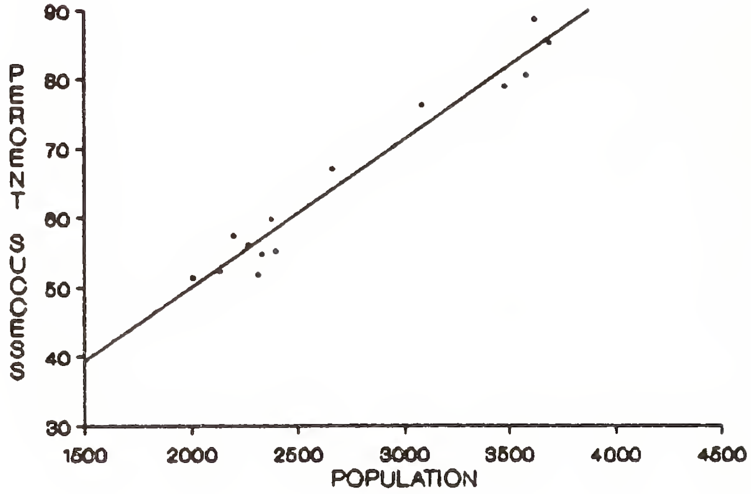
[a] 1 Kill/100 hours successful hunters.
2 Kill/100 hours all hunters (unsuccessful X 15).
3 Sightings/10 hours by successful hunters.
4 Percent hunter success.
** Permits issued daily.

Fig. 5. Indices of catch/unit effort vs model population, Crab Orchard NWR, 1974-1988 (clockwise from upper left: kill/hour all hunters, kill/hour successful hunters, percent hunter success, sightings/hour).


KILL/HOUR
30
25
20
15
10
5
1500
2000
2500
3000
3500
4000
4500
POPULATION


KILL/HOUR
14
12
10
8
6
4
2
1500
2000
2500
3000
3500
4000
4500
POPULATION


SIGHTINGS/HOUR
80
60
40
20
0
1500
2000
2500
3000
3500
4000
4500
POPULATION


PERCENT SUCCESS
90
80
70
60
50
40
30
1500
2000
2500
3000
3500
4000
4500
POPULATION

Variation D: DeLury method

Description: This method is based on a technique first described by DeLury (1947) which assumes that the log of catch/unit effort is a linear function of cumulative effort. Eberhardt (1960) modified DeLury's (1951) exponential equation to estimate prehunt population size as:

$$N_o = \frac{K}{1-e^{-cE}} \quad \text{where}$$

N_o = initial population

K = total catch

E = total effort

c = proportion of population caught by 1 unit of effort

e = base of natural logarithm

Assumptions

1. Proportion of population caught by 1 unit of effort (c) does not vary with population size.

Input

1. Estimate of total harvest.
2. Estimate of total effort.
3. Estimate of proportion of population caught by 1 unit of effort (c).

Output

1. If c is known, or can be reasonably estimated, then output is an absolute estimate of population size.

2. If a constant c is arbitrarily set, then output is a relative index of population size.

Test Data

Hunting effort from 1975 through 1988 was measured in 3 ways: permits issued, hunters afield, and hours hunted. The parameter c for each of these indices of effort was selected in 2 ways: arbitrarily, and by regressing catch/unit effort on estimated population size[1]. The resulting combinations were used to obtain 6 separate sets of population estimates (Table 5).

Results

It was not possible to evaluate the accuracy of this technique because c was not determined independently of the estimates to which it was compared. However, The method appeared to track actual population trends quite well (Fig. 6).

Discussion

Overall, this method appeared to produce a very reasonable index of population trends over time. The number of hunters afield or permits issued as measures of effort gave seemingly better results than did kill or sightings/hours. This was not unexpected as percent hunter success showed a stronger and more linear relationship with population size than did kill or sightings/hours (Fig. 5). As might also be expected, the arbitrarily-selected c values gave apparently better results than those obtained when c was selected by regression. This is probably because the latter method must assume a 0 intercept, which is theoretically logical, but did not provide the best fit of the actual data.

---

[1] If catch/unit effort is plotted against population size and a straight line fitted with a 0 intercept, the slope of that line is the proportion of the population taken with each unit of effort (this value * total effort = the instantaneous harvest rate).

References

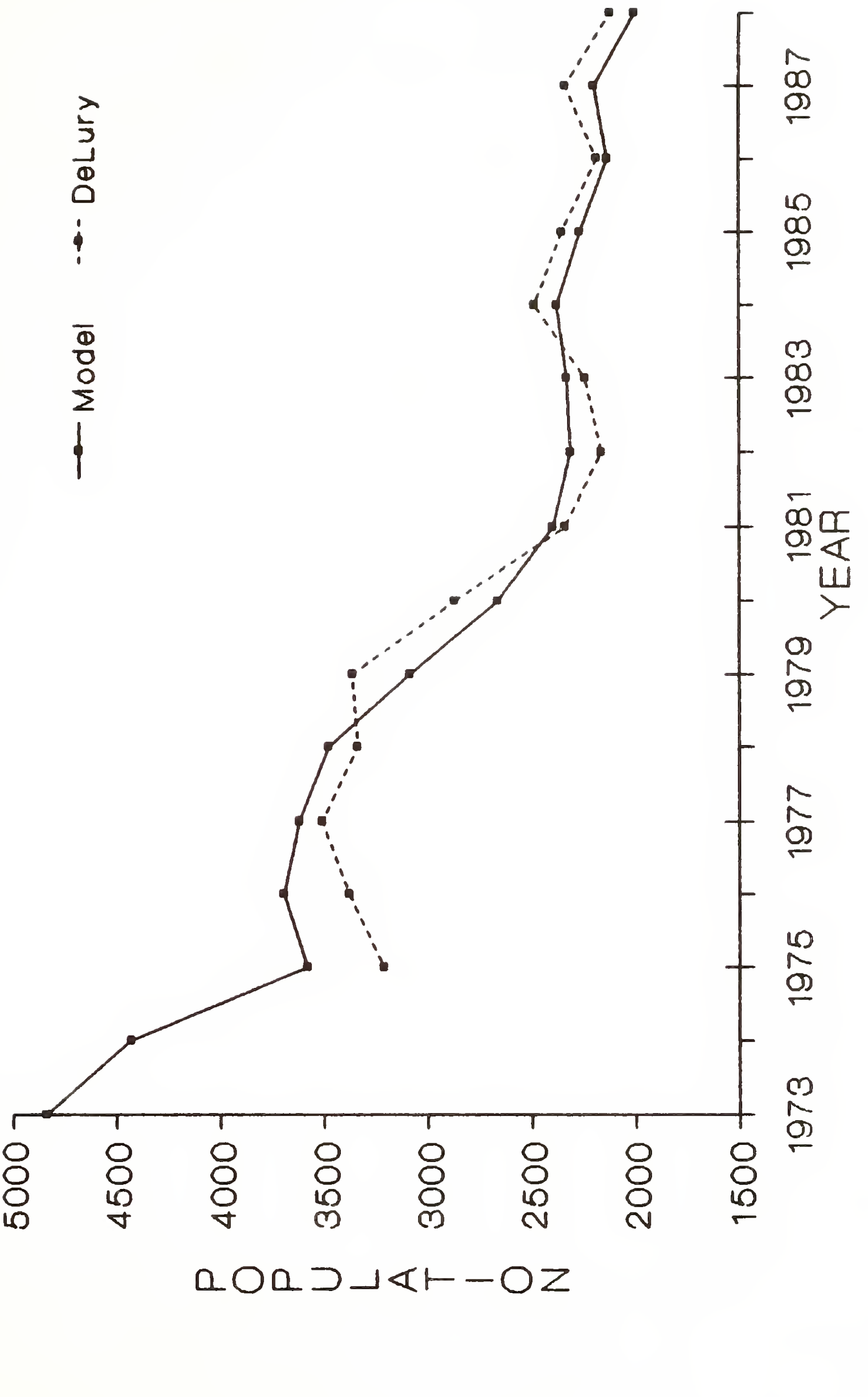
1. DeLury, 1947 (original)
2. DeLury, 1951 (original)
3. Eberhardt, 1960 (descriptive)
4. Stormer et al., 1974 (application)

Table 5. Population estimates based on DeLury's catch/unit effort technique, Crab Orchard NWR, 1975-1988.

Year	Population Size	DeLury Estimates[a]					
		1	2	3	4	5	6
1975	3578	3574	4129	3285	3672	3210	3651
1976	3690	3963	4581	3472	3881	3376	3840
1977	3616	4411	5104	3612	4037	3503	3984
1978	3475	3311	3793	3374	3750	3337	3773
1979	3084	3116	3557	3316	3679	3358	3791
1980	2661	2374	2707	2871	3191	2866	3240
1981	2394	1888	2156	2340	2604	2337	2646
1982	2310	1697	1940	2169	2416	2160	2450
1983	2328	1859	2133	2261	2522	2238	2542
1984	2375	2216	2541	2498	2784	2481	2814
1985	2263	1872	2138	2366	2634	2349	2661
1986	2130	1752	1998	2224	2474	2181	2468
1987	2194	2044	2338	2427	2702	2333	2640
1988	2003	1721	1964	2177	2422	2121	2399

[a] 1 Hours hunted by all hunters; c arbitrarily selected for best fit (0.000031).
2 Hours hunted by all hunters; c determined from regression (0.000027).
3 Hunters; c arbitrarily selected for best fit (0.00027).
4 Hunters; c determined from regression (0.00024).
5 Permits; c arbitrarily selected for best fit (0.00025).
6 Permits; c determined from regression (0.00022).

Fig. 6. DeLury catch/unit effort index and model population, Crab Orchard NWR, 1973-1988.


POPULATION
5000
4500
4000
3500
3000
2500
2000
1500
YEAR
1973
1975
1977
1979
1981
1983
1985
1987
Model
DeLury

Technique III: Population Reconstruction
(virtual population or cohort analysis)

Variation A: "Standard"

Description

This method, first proposed by Fry (1949) as a means of studying lake trout (*Salvelinus namaycush*) populations, determines the minimum possible number of individuals alive in a given cohort for a given year by summing all of the individuals from that cohort retrieved in subsequent years. For example, the minimum number of fawns alive at the beginning of hunting in year *t* can be determined by adding the fawn harvest for that year to the yearling harvest in year *t*+1, the 2.5 harvest in year *t*+2, etc. Animals found dead or assumed unretrieved can also be included, as can estimates of natural mortality. The virtual population estimate approaches reality as the proportion of each cohort ultimately recovered approaches 100%. Total estimates can be obtained by dividing minimum estimates by the assumed lifetime recover rate for the cohort involved.

Assumptions

1. The proportion of deaths accounted for is relatively constant over time.
2. Age determination is accurate.

Input

1. Evidence of mortality (e.g. hunter harvests, dead deer searches) by age class.

Output

1. Minimum (virtual) population estimates for individual cohorts or entire population.

Test Data

Annual harvest data by sex/age class for the period 1973-1988 were used to reconstruct male and female segments of the population. The 4.5+ age category was proportioned into classes 4.5, 5.5, 6.5, and 7.5 prior to reconstruction. Crippling (unrecovered) losses of 11%, 22%, and 29% were assumed for bucks, fawns, and does, respectively (Hardin and Roseberry 1976). Reconstruction of the years 1986-1988 were not attempted because cohort members were still at large. Two alternative methods were used to estimate populations for this recent period. One approach was that of Fryxell et al. (1988) who used the proportion of the population harvested by 1 unit of effort (based on previous reconstruction and harvest data) in combination with current harvest and effort estimates to obtain prehunt population size (equivalent to Variation D of the Catch Per Unit Effort technique). The second method computed an average harvest rate from previous reconstructions and harvest, then divided that rate into current harvests to obtain prehunt population size (Creed et al. 1984).

Results

Absolute population estimates agreed most closely with model output when lifetime recovery rates of 0.70 and 0.55 were assumed for males and females, respectively (Table 6, Fig. 7). Annual indices of abundance based on reconstruction appeared to be low during 1973-1975 and somewhat high during 1978-1980. Estimates for recent years based on estimated harvest rates averaged about 8% higher than those based on the catch/unit effort method.

Discussion

Minimum virtual estimates appeared to track past population trends reasonably well. However, as Downing (1980), noted, the technique was sensitive to changes in harvest intensity. Estimates tended to be low during the early 1970's when harvest rates were relatively low, and high during the late 1970's when harvest rates were increased (Fig. 7). The technique is also sensitive to aging errors. If any age class is underaged, minimum populations will be underestimated.

Absolute population estimates can be obtained from virtual minimum estimates only by assuming a lifetime recovery rate for the sex/age classes involved. Normally, the value assigned to this parameter is only an educated guess; therefore, absolute population estimates from reconstruction must be treated accordingly. We suspect that assumed lifetime recovery rates used here (0.70 and 0.55) are probably too low. However, if more realistic rates of perhaps 0.80 and 0.65 were assigned, total population estimates were too low. The tendency for reconstruction to underestimate population size is probably due in part to a tendency to underage adults at check stations.

References

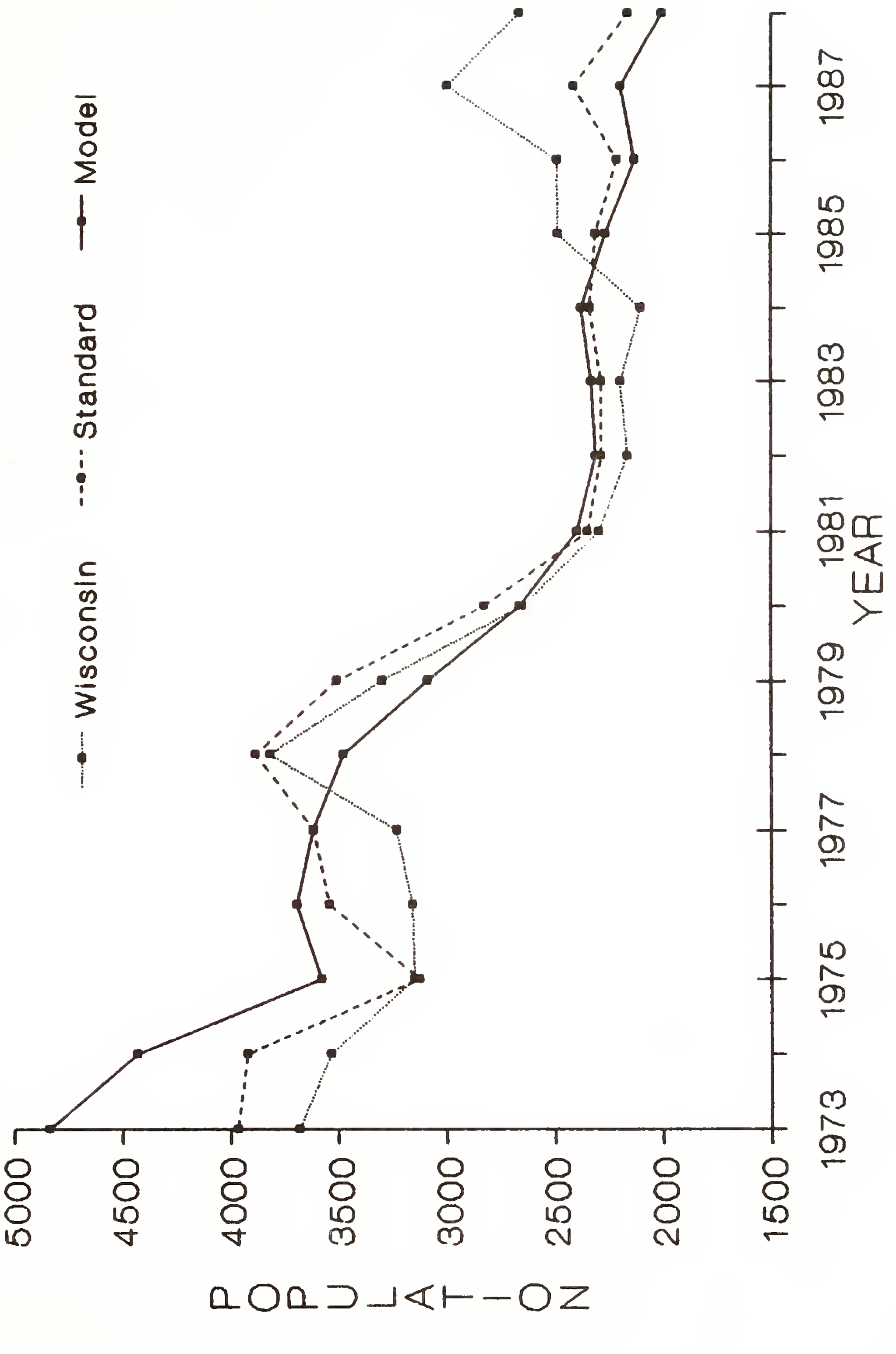
1. Fry, 1949 (original)
2. Watt, 1968 (descriptive)
3. Hesselton et al., 1965 (application)
4. McCullough, 1979 (application)
5. Woolf and Harder, 1979 (application)

Table 6. Results from various population reconstructions, Crab Orchard NWR, 1973-1988.

	Reconstruction Method[a]				
Year	1	2	3	4	5
1973	2869	3243	3423	3681	3967
1974	2704	3061	3290	3534	3921
1975	2568	2959	2912	3149	3125
1976	2435	2792	2940	3159	3543
1977	2703	3100	2974	3228	3611
1978	3072	3564	3524	3812	3879
1979	2819	3271	3045	3294	3506
1980	2114	2455	2454	2645	2823
1981	1850	2151	2130	2294	2344
1982	1644	1908	2017	2161	2282
1983	1966	2281	2036	2196	2284
1984	1568	1804	1947	2101	2336
1985	2012	2350	2322	2484	2308
1986	2231	2605	2314	2486	2210 (2432)
1987	2952	3458	2793	2993	2412 (2548)
1988	2412	2801	2464	2663	2163 (2361)

[a] 1 Wisconsin (adult males; adjusted sex ratio).
2 Wisconsin (adult males; unadjusted sex ratio).
3 Wisconsin (all males; adjusted sex ratio).
4 Wisconsin (all males; unadjusted sex ratio).
5 Standard; last 3 years based on estimate of q; last 3 years in ( ) based on harvest rate estimate; both estimates based on 1981-85 data.

Fig. 7. Population reconstruction and model population, Crab Orchard NWR, 1973-1988.


Wisconsin
Standard
Model
POPULATION
5000
4500
4000
3500
3000
2500
2000
1500
1973
1975
1977
1979
1981
1983
1985
1987
YEAR

Variation B: "Downing"

Description

This method, proposed by Downing (1980), is similar to "standard" reconstruction described above except in its treatment of the last inclusive age category. Instead of arbitrarily proportioning this category into older age classes, Downing computes survival rates based on the number of dead animals in the last 2 classes. He then uses these rates in conjunction with the number of dead animals in these classes to estimate numbers alive at the beginning of the year. Younger age classes are reconstructed normally by simple addition.

Assumptions

1. Same as Variation A.

Input

1. Same as Variation A.

Output

1. Same as Variation A.

Test Data

Same as Variation A.

Results

Downing's method produced results almost identical to those from standard reconstruction (annual deviation $\leq$ 2%).

Discussion

Downing (1980) and others (e.g. Andrews and Calhoun 1968, Fryxell et al. 1988) have suggested that in addition to providing minimum population estimates, reconstruction can be used to estimate vital population statistics such as age-specific harvest rates, fawn:doe ratios, and adult sex ratios. There are, however, several problems associated with this use. As noted earlier, reconstruction seems to overestimate fawn:doe ratios because of progressively increasing progeny/progenitor ratios with age. Reconstructed adult sex ratios, on the other hand, are dependent on arbitrarily-selected lifetime male and female harvest rates and therefore cannot be considered unbiased estimates of this statistic. Finally, harvest rates derived from reconstruction will always be too high if minimum population estimates are used. If total population estimates are used, then derived harvest rates will depend on arbitrarily-selected lifetime recovery rates. There are additional problems associated with estimation of fawn harvest rates from reconstruction. While such estimates do represent the maximum possible harvest rate, they cannot be used to monitor changes in fawn harvest rates over time or between areas. The reason is that fawn reconstruction is also affected by adult harvest rates. If harvest rates of fawns and adults are similar, the fawn harvest:fawn reconstruction ratio for a particular year will merely reflect the living fawn:adult ratio for that year, not necessarily the fawn harvest rate. If harvest rates of fawns and adults differ, then the fawn harvest rate estimate will be affected by the adult harvest rate.

References

1. Downing, 1980 (descriptive)

Variation C: "Cohort Analysis"

Description

Fryxell et al. (1988) described a technique that combines cohort analysis or reconstruction with a catch/unit effort technique to analyze moose (*Alces alces*) populations. For cohorts that have passed through the population, this technique uses standard reconstruction combined with estimates of age-specific mortality to estimate past abundance. For cohorts which have not passed through the population (recent years), a vulnerability coefficient q[2] (proportion of population killed by 1 unit of effort) is estimated for each cohort using the mean of several past year's data:

$$q = (\log e\ ((\text{reconstruction}-\text{harvest})/\text{reconstruction}))\ /\ \text{hours hunted}$$

Cohort size (N) is then computed as:

$N = K/(1 - e^{-qE})$ where

K = cohort harvest

E = total effort

Assumptions

1. Same as Variation A.
2. Harvest rate is a linear function of *q* and E.

---

[2] This is analogous to *c* used in Variation D (DeLury Method) in the Catch per Unit Effort Section, and the method of estimating population size is the same.

Input

1. Same as Variation A.
2. Independent estimate of age specific survival rates.
3. Measure of total hunting effort.

Output

1. Same as Variation A.

Test Data

Same as Variation A. Completed cohorts were reconstructed by assuming a lifetime recovery rate of 0.70 for males and 0.55 for females rather than using estimates of age specific survival.

Results

Results for completed cohorts (1973-1985) were identical to those from "standard" reconstruction. Estimates for incomplete cohorts (1986-1988) averaged 7% higher that those from the model and 8% below those based on estimated harvest rate (Table 6).

Discussion

Fryxell et al. (1988) considered their method useful for analyzing completed cohorts but cautioned against its "indiscriminate" use to estimate current levels of abundance because of problems in estimating $\underline{q}$. We would reiterate, however, that age-specific survival rates are generally not available for most deer herds, and arbitrary selection of lifetime recovery rates limits the technique to identifying trends in abundance rather than absolute population size.

Reference

1. Fryxell et al., 1988 (description, application)

Variation D: "Wisconsin"

Description:

This method uses standard reconstruction to obtain a minimum population estimate for adult males. The adult male population is then multiplied by an "expansion factor" (a measure of adult sex ratio and recruitment) to obtain an estimate of total population size (Creed et al. 1984). The procedure is as follows:

TP = AM * EF where

TP = total population

AM = adult male population

EF = expansion factor

Minimum adult male population (AM).-- This is obtained by standard reconstruction of annual harvest data. To correct for nonharvest mortality, an 80% final recovery (lifetime harvest rate) is assumed (i.e., AM = reconstruction/0.80). For years too recent to include in reconstruction, AM is estimated by dividing the male harvest for that year by the previous 3-year average of buck harvest rates (obtained by dividing actual harvest by AM for that year).

Expansion factor (EF).-- Calculated as:

EF = 1.00 + FA:MA + ((FA:MA)*(F:D)) where

FA:MA is the adjusted adult female/adult male ratio[3], and

F:D is the fawn:doe ratio from summer observations

Assumptions

1. The proportion of deaths accounted for is relatively constant over time.
2. Age determination is accurate.
3. Estimates of adult sex ratio and fawn:doe ratio are accurate.

Input

1. Evidence of mortality (e.g. hunter harvests, dead deer searches) by age class.
2. Estimate of productivity (fawn:doe ratio).

Output

1. Estimate of absolute population size.

Test Data

Input data for the above method was 1973-1988 CONWR harvests by sex/age class. A 0.70 lifetime recovery rate for males was used to make results comparable to Variation A. Several alternative ways of estimating parameters were tested. These were:

---

[3] Calculation of FA:MA follows Severinghaus and Maguire (1955); i.e., (proportion of yearlings among adult males)/(proportion of yearlings among adult females). This ratio is then "adjusted" for suspected unequal recruitment into the yearling class by dividing by the male fawn:female fawn harvest ratio.

a) Reconstruction of the total male population rather than just adult males (in this case, the "expansion factor" (EF) represented the entire population sex ratio[4] and did not include the recruitment component.

b) Adult sex ratio based on average of past 3 years data rather than current years statistics.

c) Adult sex ratio not "adjusted" for possible unequal recruitment into yearling cohort.

d) Fawn/doe ratios obtained from harvest rather than observation data.

Results

Population estimates were generally low, especially during the early years, whereas estimates for the last 3 years (based on estimated harvest rate) were too high (Table 6, Fig. 7). Annual estimates for completed cohorts (1973-1985) averaged 8% below those from "standard" (Variation A) reconstruction. Comparative results from the various alternatives are described below:

a) Reconstruction of adult males produced estimates that averaged 5-13% lower than those based on reconstruction of the entire male population.

b) Use of a 3-year average rather than current values produced similar results (the latter are presented in Table 6).

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[4] [0.96(proportion fawns in harvest)] + [(FA:MA(proportion adults in harvest)]

c) Results from "adjusted" adult sex ratios (for unequal recruitment into yearling class) averaged 8-16% lower than those using non-adjusted ratios.

d) Population estimates from runs using observational rather than harvest fawn:doe ratios averaged 14% lower.

Discussion

This variation produced estimates for completed cohorts than averaged 8% below those from "standard" reconstruction (Table 6). With regard to the alternative ways of computing parameters for the EF factor, we recommend using harvest fawn:doe ratios rather than observational data which are negatively biased. However, in places such as Illinois where any-deer seasons are traditional, reconstructing the entire male population seems preferable to reconstructing the adult segment only. In this case, fawn:doe ratios are not needed. Finally, if annual fawn harvests are heavy enough so that harvest bias toward males tends to balance male:female recruitment into the yearling class, then "adjustment" of the FA:MA ratio is not recommended.

Reference

Creed et al., 1984 (variation)

Technique IV: Change-In-Ratio (CIR)

Variation A: "Kelker"

Description

Kelker (1940) first described this method of estimating deer abundance based on differential harvest of the sexes. If there is selective removal of a particular type of animal, and if the proportion of that type in the population can be estimated before and after removal, then preremoval population size can be estimated as follows:

$$N = \frac{R_x - RA}{B - A}$$ where

$N =$ population size prior to removal

$R_x =$ number of x-type animals removed

$R =$ total number of animals removed

$B =$ proportion of x-type animals before removal

$A =$ proportion of x-type animals after removal

Assumptions

1. x- and y-type animals are sampled with equal probability during the "before" and "after" periods.
2. The population is closed between periods except for known removals.
3. The proportion of x-type animals in the harvest is different then in the pre-removal population (i.e., removal is selective).

Input

1. Estimate of total harvest and representation of x- and y-type animals in harvest.
2. Estimate of pre and posthunt representation of x- and y-types.

Output

1. Estimate of absolute population size.

Test Data

Pre and posthunt ratios were obtained from fall and winter roadside counts. Removals were based on recorded hunter harvests plus estimated crippling loss. Two types of ratios were originally tested: a) buck/doe (proportion of bucks in adult population), and b) antlered/antlerless (proportion of bucks in total population). Downing et al. (1977) recommended the latter because of larger sample sizes and less opportunity for error (e.g. mistaking yearling females for fawns). We agree and use the antlered/antlerless ratio hereafter.

Results

Overall, the CIR technique performed very poorly, both in terms of estimating absolute population size and monitoring trends (Table 7).

Discussion

There appeared to be 2 serious problems with application of CIR to the CONWR data. First, the assumption of equality of "before and after" observations was violated. Even prior to hunting (1967-1972), autumn ratios were consistently different (usually lower) than those obtained in winter.

Several workers (Hirth 1977, Downing et al. 1977, McCullough 1982, Sage et al. 1983) have noted that observability of bucks varies seasonally. In addition, both seasonal ratios were probably both biased. Dasmann (1952:227) noted that small errors in ratios can make large differences in population estimates. According to Downing (1980), this effect is less if the sex ratio of the harvest is greatly different that the observed ratio (i.e., harvest highly selective). On CONWR, representation of bucks in the harvest was almost twice that of prehunt observations.

Conner et al. (1986) discussed sample sizes (number of animals classified in observations) necessary to achieve given levels of accuracy and precision with various values of $\underline{B}$ and changes from $\underline{B}$ to $\underline{A}$. They noted, for example, that if $\underline{B} \leq 0.10$ (CONWR $\bar{X} = 0.13$), then pre and post sample sizes of 1600 should give population estimates ± 25% 95% of the time (if $\underline{B}$ and $\underline{A}$ not inherently different). The number of observations during pre and post hunt observations on CONWR averaged approximately 1100 with nearly 80% between 500 to 1500.

Necessary prerequisites for accurate CIR estimates were met or approached on CONWR in terms of differences in harvest and observed ratios and numbers classified during observations. Therefore, we conclude that the technique's poor performance primarily reflected differential observability of males during the 2 periods. Based on the above, we would tend to agree with Dasmann's (1952) essentially negative assessment of the technique for deer rather than the more positive endorsement of Conner et al. (1986).

References

1. Kelker, 1940 (original)
2. Kelker, 1944 (application)

3. Dasmann, 1952 (application)
4. Chapman, 1955 (descriptive)
5. Paulik and Robson, 1969 (descriptive)
6. Downing et al., 1977 (evaluation)
7. Downing, 1980 (descriptive)
8. Conner et al., 1986 (application)

Table 7. CIR (Variation A, B) population and harvest rate estimates, Crab Orchard NWR, 1973-88.

Year	B	A	K	Harvest Rate Bucks	Antlerless	Total	N
1973	0.139	0.082	0.416	0.511	0.116	0.172	5595
1974	0.186	0.056	0.358	0.829	0.339	0.430	3165
1975	0.199	0.081	0.397	0.743	0.280	0.372	1896
1976	0.147	0.025	0.388	0.885	0.240	0.335	2225
1977	0.137	0.034	0.435	0.814	0.168	0.256	2975
1978	0.100	0.087	0.328	0.186	0.042	0.057	18701
1979	0.113	0.074	0.297	0.457	0.137	0.173	6634
1980	0.132	0.020	0.295	0.909	0.329	0.405	2259
1981	0.091	0.057	0.291	0.466	0.114	0.146	4792
1982	0.135	0.047	0.290	0.781	0.299	0.364	1619
1983	0.127	0.061	0.349	0.628	0.170	0.228	2410
1984	0.102	0.062	0.321	0.491	0.118	0.156	4309
1985	0.124	0.052	0.278	0.715	0.262	0.318	2163
1986	0.103	0.058	0.309	0.545	0.141	0.182	3677
1987	0.121	0.043	0.354	0.737	0.185	0.251	2775

B = Proportion bucks in prehunt census.
A = Proportion bucks in posthunt census.
K = Proportion bucks in harvest.
N = Prehunt population size.

Variation B: "Petrides (Selleck-Hart)"

Description:

Sometimes referred to as the Selleck-Hart method, this technique was first described by Petrides (1954). If the basic assumptions of CIR are met, then harvest rates of x- and y-type animals can be calculated by comparing their relative proportion in the population before, during, and after harvest. The procedure is as follows:

$\frac{(B - A)}{(K - A)}$ = harvest rate of total population, and

$\frac{K(B - A)}{B(K - A)}$ = harvest rate of x-type animals, and

$\frac{K'(B - A)}{B'(K - A)}$ = harvest rate for y-type animals· where

B = prehunt proportion of x-type animals

B'= prehunt proportion of y-type animals

K = proportion of x-type animals in harvest

K'= proportion of y-type animals in harvest

A = posthunt proportion of x-type animals

Assumptions

1. Same as Variation A.

Input

1. Same as Variation A.

Output

1. Estimate of harvest rate for x- and y-type animals.
2. Estimate of absolute population size for x- and y-type animals.

(obtained by dividing harvest rates into the numerical harvest). These are exactly the same as those produced by Variation A.

Test Data

Same as Variation A.

Results

This method gave average annual harvest rates (including crippling) of .646 and .256 for antlered and antlerless deer, respectively. These estimates may not be too unrealistic; in fact, the long-term average anterless harvest rate suggested by the model was .235. However, annual CIR estimates were erratic (range .042 to .339) and did not track expected trends (Table 7). Derived population estimates were the same as those from Variation A, and were equally unsatisfactory.

Discussion

Reasons for the poor performance of this technique are the same as those described for Variation A.

References

1. Petrides, 1954 (original)
2. Selleck and Hart, 1957 (descriptive)

Variation C: "Shope"

Description

This method combines CIR with age structure data to estimate population size (Shope 1978). The principle variation is that pre- and posthunt ratios are estimated from harvest data rather than observations. The procedure is as follows:

1. Prehunt adult males:100 adult females (B) calculated from Year 1 harvest data using the Severinghaus-Maguire (1955) technique (no adjustment for unequal recruitment).
2. Posthunt adult males:100 adult females (A) calculated from Year 2 harvest using a variation of the Severinghuas-Maguire (1955) technique:

$$\frac{\%2.5+ \text{ males X } \%1.5 \text{ females}}{\%1.5 \text{ males X } \%2.5+ \text{ females}}$$

3. Male harvest rate computed using Selleck-Hart CIR (Variation B).
4. Prehunt adult male population in Year 1 obtained by dividing number of bucks harvested by harvest rate.
5. Prehunt adult male population combined with B to obtain prehunt adult female population.
6. Minimum fawn population (fawns recruited into Year 1 prehunt population) computed by solving for X in the following equation:

$$\frac{\text{X - female fawn harvest}}{\text{prehunt ad female - ad female harvest}} = \frac{\%1.5 \text{ female in Year 2 hv}}{\%2.5 \text{ female in Year 2 hv}}$$

where X = prehunt female fawn population, and

2X = prehunt total fawn population

The procedure for estimating next year's prehunt population is as follows:

1. Above population estimates are calculated for past several years.

2. Annual adult mortality rates are computed from posthunt populations in Year 1 and prehunt populations in Year 2.
3. Annual mortality rates are regressed on corresponding posthunt densities.
4. Regression equation then used to estimate adult mortality based on posthunt population of the current year.
5. Estimated adult mortality combined with posthunt population of current year to estimate prehunt adult population in following year.
6. Average minimum fawn production rate then combined with posthunt population to estimate recruitment.
7. Recruitment added to prehunt adult population to give estimate of total population for coming year.

Assumptions

1. Calculation of $\underline{B}$ requires that yearling males and females be recruited equally into the fall population and that they be harvested at a similar rate.
2. Calculation of $\underline{A}$ requires that male and female fawns be equally represented in the posthunt population.
3. Calculation of minimum fawn population requires equal harvest rate for fawns and does as well as equal natural mortality rate to the next autumn.

Input

1. Harvest data by sex and age class at least thru 2.5 years.

Output

1. Estimate of absolute population size.
2. Projection for the following year.

Test Data

This method was tested using CONWR harvest data with and without estimated crippling loss.

Results

Neither dataset produced satisfactory results (Table 8). Annual population estimates (assuming crippling loss) ranged from 946 to 6811 and did not appear to follow general trends over time.

Discussion

Population estimates from this method seemed generally low and showed large variation from year to year. The latter probably reflects Dasmann's (1952) warning that small errors in ratios can give large differences in population estimates. The former probably reflects more systematic biases in the pre- and posthunt ratios. If proportionately more yearling males than yearling females are harvested (which is apparently the case), then the prehunt sex ratio is biased toward males which causes harvest estimates of both sexes to be too low and population estimates to be too high. The posthunt sex ratio is affected oppositely, i.e., toward females, causing harvest rate estimates to be too high and population estimates too low. Seemingly, these biases should cancel each other out; however, it can be shown that the posthunt ratio is relatively more affected than the prehunt ratio thus biasing the population estimate downward.

Reference

1. Shope, 1978 (original)

Table 8. CIR (Variation C) estimates for Crab Orchard NWR, 1973-1987.

	Parameters[a]						
Year	B	A	AMHR	AMP	AFP	FFP	TOT
1973	0.891	0.778	0.327	1109	1244	1268	3621
1974	0.857	0.428	0.888	498	580	424	1502
1975	0.591	0.526	0.189	1349	2284	3178	6811
1976	0.724	0.418	0.625	420	579	586	1585
1977	0.623	0.297	0.668	451	723	460	1634
1978	0.461	0.199	0.731	433	939	762	2134
1979	0.443	0.239	0.680	456	1029	834	2319
1980	0.462	0.155	0.830	296	640	646	1582
1981	0.452	0.215	0.722	256	566	642	1464
1982	0.529	0.190	0.825	189	357	400	946
1983	0.500	0.349	0.452	386	771	816	1973
1984	0.580	0.203	0.857	228	392	302	922
1985	0.433	0.138	0.819	212	489	484	1185
1986	0.424	0.204	0.669	280	660	570	1510
1987	0.434	0.228	0.575	391	899	1014	2304

[a] B Adult male:adult female in prehunt population.
A Adult male:adult female in posthunt population.
AMHR Adult male harvest rate.
AMP Adult male prehunt population.
AFP Adult female prehunt population.
FFP Fawn prehunt population.
TOT Total prehunt population.

Variation D: "Nevada"

Description

Hess (1985) described a method developed for mule deer management in Nevada which combines the Selleck-Hart CIR with harvest, posthunt census, and fawn production data to obtain population estimates. The primary variation is that prehunt ratios are obtained not from independent observations, but from the previous year's calculations. The procedure is as follows:

1. Antlered and antlerless harvest rates computed by Selleck-Hart CIR (Variation B), then divided into total harvest to obtain prehunt population estimates for Year 1.
2. Post-hunt population obtained by subtracting harvest from prehunt population.
3. Spring adult population computed from posthunt population and estimate of winter mortality (winter mortality and fawn:adult ratios obtained from posthunt and spring censuses).
4. Summer fawn production estimated from spring adult population size and fawn:adult ratio.
5. Prehunt population in Year 2 estimated by adding spring adult population to fawns produced (sexes kept separate).
6. Prehunt sex ratio obtained from Step 5 then combined with Year 2 harvest and posthunt census to obtain estimated harvest rates using CIR (Step 1). Estimated harvest rates then combined with total harvest to estimate prehunt population in Year 2. (This estimate is independent of the one obtained in Step 5 and is used as a check).

Assumptions

1. Same as Variation A; the remainder are according to Hess (1985)
2. Natural mortality is proportionally sex independent.
3. Immigration and emigration are proportionally sex independent.
4. Natality is sex independent.
5. Yearling survival is sex independent.
6. Crippling loss can be estimated or is negligible.
7. Doe kill can be estimated or is negligible.
8. Unreported kill can be estimated or is negligible.
9. Herd units are identifiable during periods of data collection.

Input

1. Harvest data by sex.
2. Posthunt and spring census data providing buck:doe and fawn:adult ratios.

Output

1. Absolute population estimates for the current and following year.

Test Data

This method could not be tested with available CONWR data.

Discussion

According to Hess (1985), the above method was applied to individual management units in Nevada. Even the acknowledged best data set had 80% confidence limits of ± 42%. The author stated that: ". . . much of this imprecision was identified as inherent to the CIR method since the variance in input samples has a cumulative effect."

Reference

1. Hess, 1985 (original)

Technique V: Life Table Analysis

Description

Life table analysis was originally developed by actuaries as a means of analyzing human mortality and survival patterns using age frequency at death. Deevey (1947) applied the technique to various wildlife populations including a large set of Dall sheep (*Ovis* *d.* *dalli*) skulls found in the field by Murie (1944). Appropriate life table methodologies depend on whether age structure of the living or dead is being sampled, and whether the life table is dynamic (history of a single cohort over time) or time-specific (a one-time sample of all age classes). Caughley (1977) described life table procedures for various types of samples including harvest data.

Assumptions

1. The harvested sample is an unbiased estimate of the living age structure.
2. The age distribution is stable, i.e., age frequencies have been relatively constant over the preceding several years.

Input

1. Age frequencies of the harvested sample for 1 or both sexes[5].

---

[5] Input suitable only for a time-specific life table designed to analyze the living age structure (see Caughley 1977).

Output

1. Probability at birth of surviving to a given age (l_x).
2. Probability of dying in each age interval (d_x).
3. Mortality rate for each age class (q_x).
4. Mean expectation of further life at any given age (e_x).

Test Data

Harvest age frequencies of the female segment were analyzed using Caughley's (1977) Method 6. Two separate runs were made with rate of increase ($\underline{r}$) = 0 and = the previous 3-year mean from model. Because the 2.5-year class sometimes exceeded 1.5-year-olds in the harvest, it was necessary to smooth age frequencies using the log polynomial method (Caughley 1977).

Results

The mean expectation of further life for the autumn fawn class (e_x) and the average mortality rate for all females (q_x) were compared with the female harvest rate for the current and previous year using correlation analysis. Life table parameters from runs which assumed $\underline{r} = 0$ were not correlated with either current or previous harvest rates ($\underline{P} > 0.10$). E_x and q_x calculated with knowledge of $\underline{r}$ were correlated ($\underline{P} < 0.01$) with the previous year's female harvest rate ($r = -0.65$ and $+0.61$, respectively) over all years; however, when 1973 was removed (previous harvest rate = 0), the relationship was virtually nonexistent (Fig. 8).

Discussion

Life tables have been recommended for analyses of ungulate populations by Quick (1962, 1963) and Conley (1978), but others disagree. Caughley

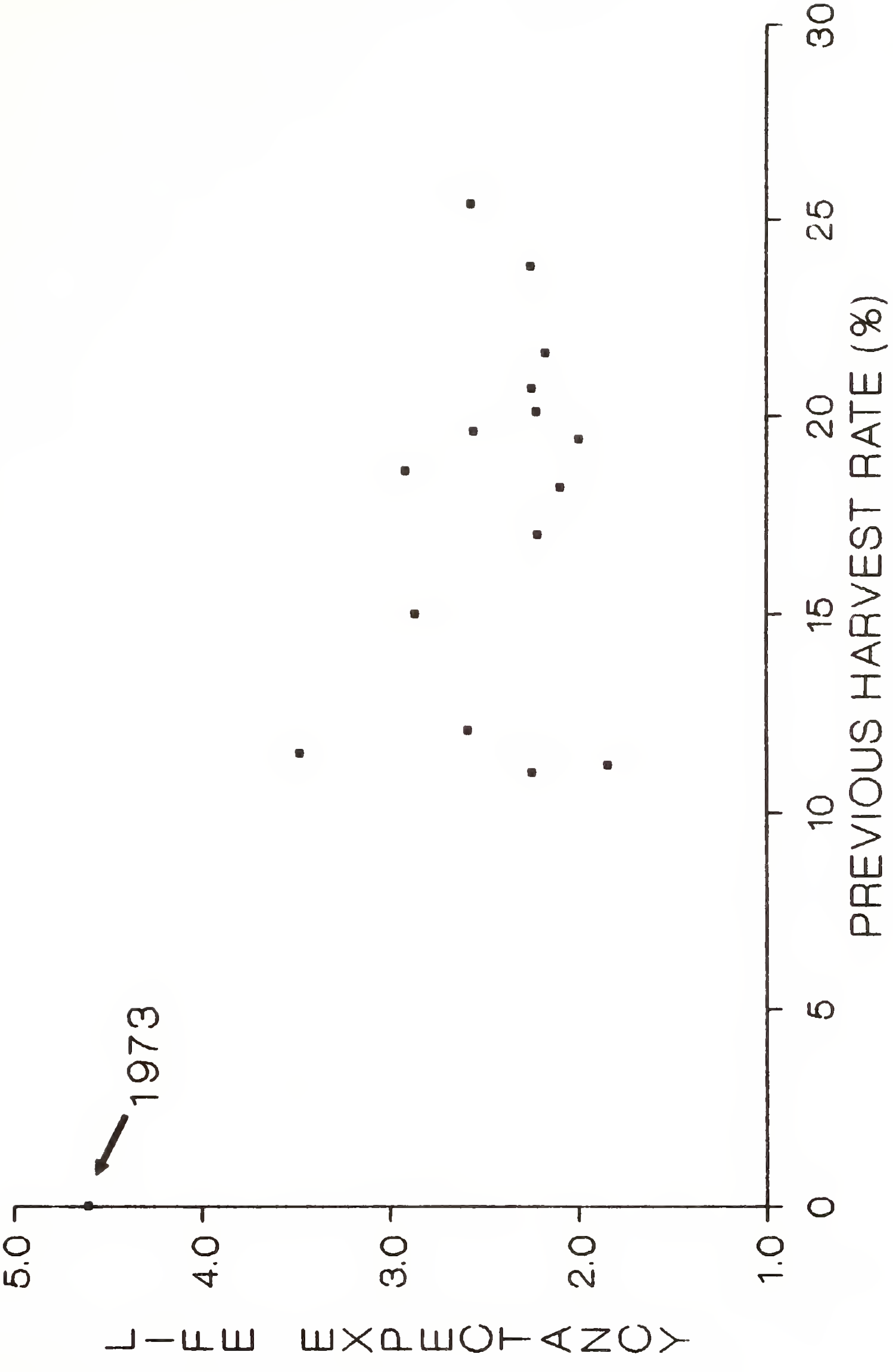
(1966, 1977) described serious problems in use and interpretation of life tables. McCullough (1979:77) found them a "disappointment" for study of the George Reserve deer herd, while Downing (1980:256) warned that calculation of survival and mortality rates using traditional life table methods "invites confusion and should be discontinued." The 2 principal drawbacks according to Caughley (1966) and McCullough (1979) are that 1) the vital assumption of stable age distrubtion is often violated in natural populations, and 2) even when all assumptions are met, life tables provide relatively little information about a population, specifically, its size and rate of growth, although there is some disagreement about the latter. Caughley and Birch (1971) and Caughley (1977) stated that $\underline{r}$ cannot be estimated from fecundity data and standing age distribution, but Michod and Anderson (1980) maintain otherwise (see also Pielou 1982 and Taylor and Carley 1988).

As noted, we calculated life table statistics for the CONWR herd both with and without annual estimates of $\underline{r}$. In the latter case, the method appeared to give no information regarding changing harvest rates or population size. When age distribution was smoothed and adjusted for estimated $\underline{r}$, e_x for female fawns and mean q_x for all females were correlated with previous harvest rate only when the 1st year (previous harvest rate = 0) was included. After that, no relationship existed, even during the period 1981-1988 when female age structure was relatively stable (Fig 8). Based on the above, we would agree with those who consider life tables to be generally unsatisfactory for analyzing white-tailed deer harvest data. Furthermore, we believe that if age-specific fecundity data are available for a particular herd, they can be better used in predictive population models rather than attempting to deal with the complexities of life table analysis.

References

1. Deevey, 1947
2. Quick, 1962, 1963
3. Caughley, 1966
4. Conley, 1978
5. McCullough, 1979

Fig. 8. Mean expectancy of further life for female fawns vs previous female harvest rate ($r = -0.65$, $P < 0.01$ with 1973; $r = -0.21$, $P > 0.20$ without 1973).


LIFE EXPECTANCY
5.0
4.0
3.0
2.0
1.0
1973
0
5
10
15
20
25
30
PREVIOUS HARVEST RATE (%)

Technique VI: Harvest Age Ratios

Variation A: Male Survival Rates

Description

Hayne and Eberhardt (1952) proposed a method similar to life table analysis for using age distribution of harvested deer (kill curves) to estimate survival rates. They noted that under certain circumstances, the log of frequencies in each age class plotted against age is a straight line, the slope of which equals the logarithm of the rate of survival. Similar results for a given age class can be obtained by simply dividing the age distribution of all older classes by the age distribution beginning with the class in question.

Several variations of this approach have been proposed. Lang and Wood (1976) use the formula:

$$\frac{1.5 - 3.5}{1.5 + 2.5 + 3.5}$$

to estimate an "average annual reduction rate" (from all causes) for harvested bucks. Downing (1980) suggested an alternative formula which is analogous to the Hayne-Eberhardt method:

$$1 - \frac{2.5 + 3.5+}{1.5 + 2.5 + 3.5+}$$

Downing (pers. comm) pointed out that this particular formula estimates mortality only for the 1.5 age class (the one missing in the numerator) not all adults. An alternative approach (Burgoyne 1981) is simply to calculate the percentage of yearlings in the buck harvest.

Assumptions

1. Equal recruitment into the male population each year.
2. Equal vulnerability to hunting among the age classes.
3. Constant survival rates over time.

Input

1. Age structure of harvested males; or at minimum, the proportion of yearlings to adults.

Output

1. Survival/mortality estimates for various age classes of males.

Test Data

Lang and Wood's (1976) "average annual reduction rate" and annual mortality rate estimates for yearling males (Downing 1980) were calculated using CONWR male harvest data 1973-1988.

Results

There was a very strong correlation (r = +0.99) between the 2 indices, with the Lang-Wood method consistently producing lower estimates.

Discussion

If the necessary assumptions are met, the Hayne-Eberhardt, Downing, and Burgoyne methods provide unbiased estimates of mortality rates, while the Lang-Wood method underestimates mortality. All of the methods overestimate mortality if the population is increasing and underestimate it if the population is declining. If yearling are overrepresented in the male harvest as apparently occurs (Roseberry and Woolf 1988), their mortality rates will be overestimated unless the harvest constitutes a major portion of annual losses.

References

1. Hayne and Eberhardt, 1952 (original)
2. Lang and Wood, 1976 (application, variation)
3. Downing, 1980 (descriptive)
4. Burgoyne, 1981 (application, variation)

Variation B: Direct Interpretation

Description/Assumptions:

This approach is based on the premise that changes in population age structure are indicative of changes in harvest rate, growth rate, and/or relative density with respect to carrying capacity.

Input

1. Frequencies by yearly age class or at least by fawns, yearlings, and adults.

Output

1. Index of population status.

Test Data

Various indices of age structure (primary, secondary age ratios, percent yearlings, mean age) were computed from annual harvest data, 1973-1988 (Appendix D). The indices were then compared with current population size, recent population change, and the previous year's sex-specific harvest rate by correlation analysis (Table 9).

Results

Mean age of males was positively related ($\underline{P} < 0.01$) with current population size ($r = +0.89$), recent population change ($r = +0.77$) and the previous year's male harvest rate ($r = -0.72$). In contrast, mean age of females was not related to any of these parameters ($\underline{P} > 0.20$). The proportion of yearlings among adult males was negatively correlated ($\underline{P}$ <

0.01) with population size (r = -0.90; Fig. 9), recent population change (r = -0.72), and previous male harvest rate (r = +0.64), whereas the proportion of yearlings among adult females was not related to any of these parameters ($P > 0.20$). The primary sex ratio among males (fawns:all older deer) was negatively correlated ($P < 0.01$) with current population size (r = -0.67) as was the primary sex ratio among females (r = -0.75) (Fig. 10). The latter index was also postively related to the previous female harvest rate (r = +0.65).

Discussion

There has been much confusion and disagreement in the literature regarding the interpretation of population age structure. The traditional view of age pyramids (e.g. Odum 1971), suggests that a growing population will be characterized by a large proportion of young animals whereas a stable population will have an older age structure. Downing (1980) and Burgoyne (1981), however, pointed out that this does not necessarily apply to exploited populations. Populations which are declining or being held at low densities by hunting often have very young age structures.

Two contrasting views on the utility of age ratios are presented by Caughley and Burgoyne. Caughley (1974:562) wrote: "Age ratios cannot be interpreted without a knowledge of rate of increase, and if we have an estimate of this rate we do not need age ratios." Burgoyne (1981:412), however, felt that: ". . . the composition of the harvest of antlered males gives a direct indication of the overall mortality rate affecting this segment of the population . . . the proportion of yearling males in the antlered harvest can be an estimate of the proportion lost annually . . ." While it is true that the percentage of yearlings in the buck harvest is a general indicator of that segment's annual mortality (and thus harvest) rate, Caughley's point may be valid. For example, there was a strong negative correlation between population size and percentage of yearlings in the CONWR buck harvest (Fig. 9), apparently because the male harvest rate generally followed trends in the antlerless harvest as well. As will be shown later, there has also been a general increase in the proportion of yearlings in regional Illinois male harvests. Inferring from the CONWR situation, one would assume that statewide populations have declined as well. However, just the opposite is true. Apparently, while there has been a general increase in the harvest rate of yearling and adult males, the harvest rate of females has actually declined. Evidence for this will be presented in a later section on Regional Herds.

Finally, there is the matter of differential interpretation of male and female age structure. Hayne and Eberhardt's (1952) method of calculating survival rates from age distribution used males in the example, but the authors did not indicate that the technique applied to that sex only. Gill (1953), however, made the important point that age structure of the 2 sexes must be interpreted differently. Specifically, age structure of the male segment reflects survival (if certain assumptions are met), while age structure of females reflects reproduction and rearing success. The reason for this is that recruitment of males is generally independent of male population size whereas recruitment of females is dependent on female population size. Burgoyne (1981) used simple models to demonstrate and confirm Gill's contention, while our data provided support. Mean age of the male segment and proportion of yearlings was correlated with population size, recent population change, and previous harvest rate while the same indices for females showed no relationship to these parameters.

The only index of female age structure related to population size and harvest rate was the primary age structure (i.e. the fawn:doe ratio). This relationship was apparently not due to changes in female survival, but to density-dependent changes in recruitment rates.

References:

1. Hayne and Eberhardt, 1952
2. Gill, 1953
3. Caughley, 1974
4. Burgoyne, 1981
5. Downing, 1980

Table 9. Correlation coefficients for indices of harvest age structure and population size, population change, and harvest rates, Crab Orchard NWR, 1963-1988.

	Primary Age Ratio[a]		Proportion Yearlings		Mean Age	
	Male	Female	Male	Female	Male	Female
Population size	-0.67 <0.01	-0.75 <0.001	-0.90 <0.001	-0.06 >0.10	+0.89 <0.001	+0.19 >0.10
Population change[b]	-0.37 >0.10	-0.41 >0.10	-0.72 <0.01	-0.17 >0.10	+0.77 <0.001	+0.26 >0.10
Previous harvest rate[c]	+0.38 >0.10	+0.65 <0.10	+0.64 <0.10	-0.14 >0.10	-0.72 <0.10	+0.10 >0.10

[a] Fawns:all older deer.
[b] Mean of 3 previous years.
[c] Of appropriate sex.

Fig. 9. Percent yearlings in annual male harvests vs model population, Crab Orchard NWR, 1973-1988.

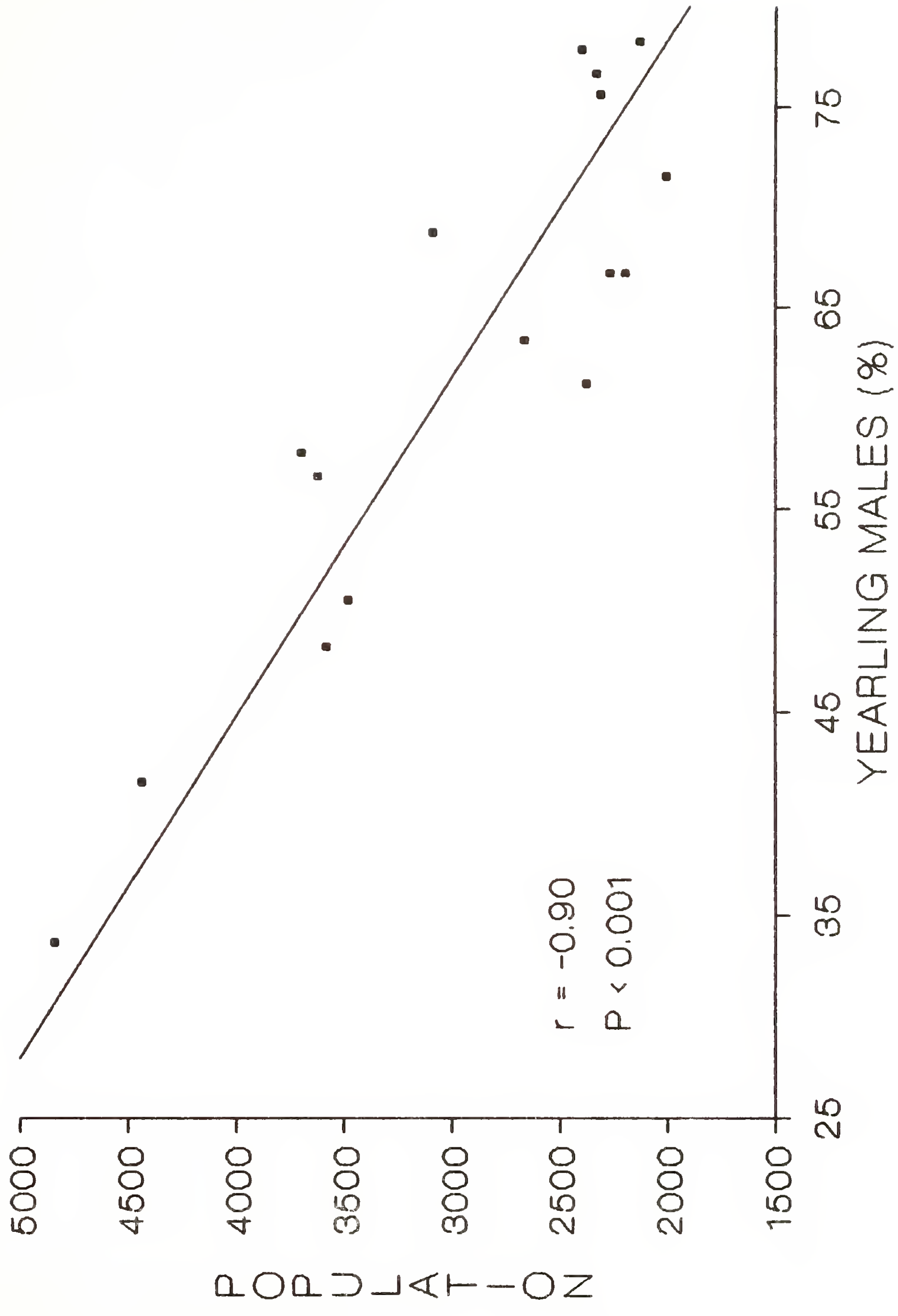
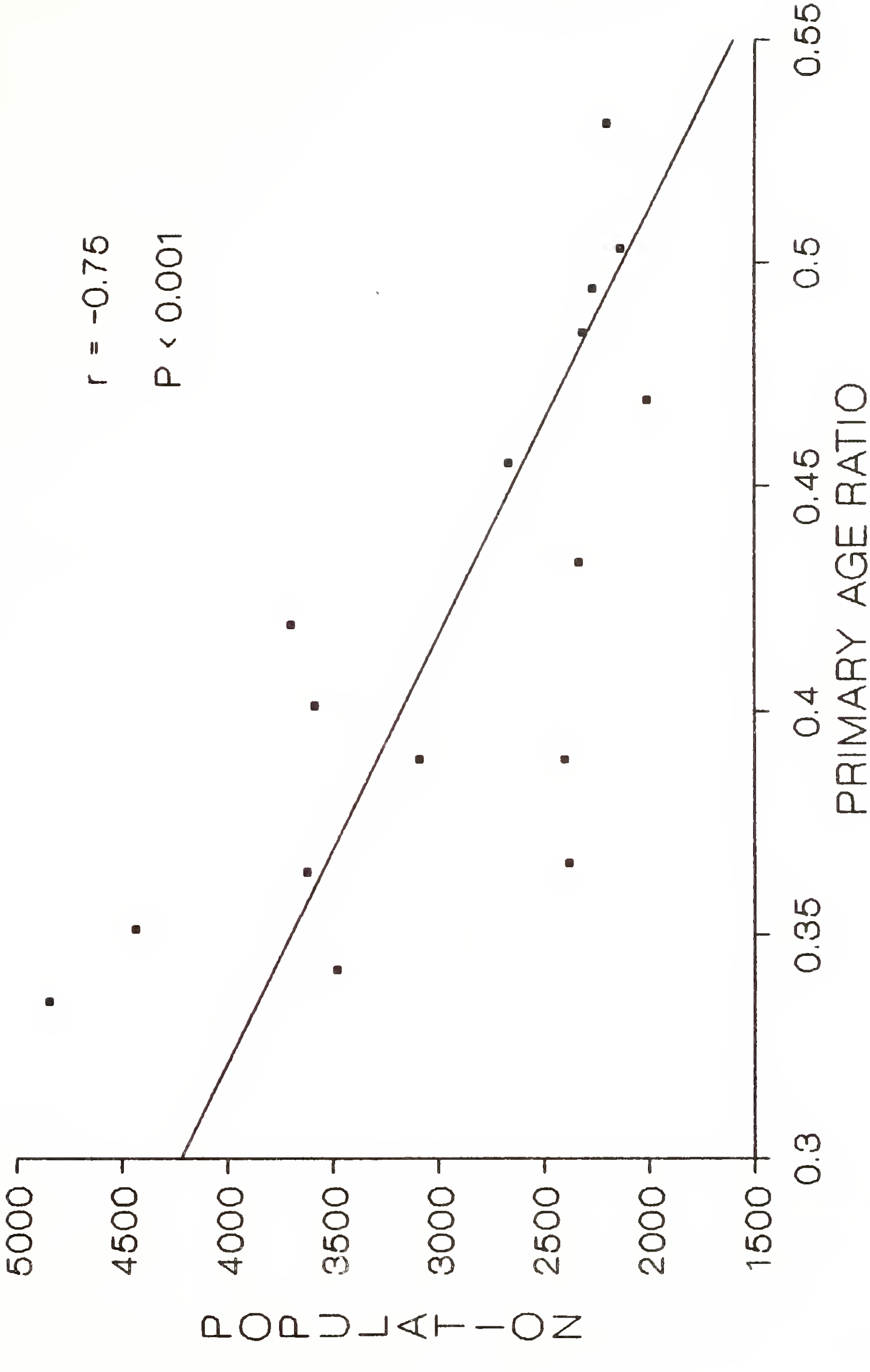

POPULATION
5000
4500
4000
3500
3000
2500
2000
1500
25
35
45
55
65
75
YEARLING MALES (%)
r = -0.90
P < 0.001

Fig. 10. Female fawn:doe ratio vs model population, Crab Orchard NWR, 1973-1988.


r = -0.75
P < 0.001
PRIMARY AGE RATIO
0.3
0.35
0.4
0.45
0.5
0.55
POPULATION
5000
4500
4000
3500
3000
2500
2000
1500

Technique VII: Harvest Sex Ratio

Variation A: "White"

Description

Laramie and White (1964) first proposed that the percentage of females in the harvest could serve as an index to relative harvest intensity.

Assumptions

1. Differential vulnerability of males and females to harvest changes as the season progresses due to behavior, availability, and hunter selectivity.
2. This differential vulnerability and its pattern of seasonal change remains relatively constant from year to year.

Input

1. Proportion of females in the harvest.

Output

1. Index of relative harvest rate.

Test Data

The annual percentage of females in the CONWR harvest (1973-1988) was compared with the estimated harvest rates for the entire herd and for the female segment (Table 10, Fig. 11).

Results

The percentage of females in annual harvests was positively correlated with harvest rate for the entire population (r = +0.60; $P < 0.05$) and especially the female segment (r = +0.80; $P < 0.001$). These relationships were even stronger prior to the last 2 years of study.

Discussion

Antlered males tend to predominate in early-season harvests (Severinghaus and Cheatum 1956) with a corresponding progressive increase in representation of females (White and Banasiak 1962). This pattern has also been observed in CONWR (Roseberry and Klimstra 1974) and statewide Illinois deer harvests (Roseberry and Woolf 1988). The latter authors suggested it was due to: ". . . a seasonal decline in availability of males following initial disproportionate harvest coupled with (and related to) an initial negative bias against fawns and females that diminished as the season progressed." White (1968) noted that in New Hampshire, males predominated in areas of light harvest and females in areas of heavy harvest, while Holbrook (1986) reported a positive correlation between percent females in the harvest and length of any-deer seasons in Georgia. The logical hypothesis to derive from this is that percent females in the harvest is correlated with overall harvest rate (White 1968). As noted above, this was indeed the case on CONWR. However, based on simulations by Downing (1981), use of percent females in the harvest to compare harvest rates among different areas or populations would probably not be justified.

The percentage females in the last 2 CONWR harvests were lower than expected, possibly because of an unusually heavy fawn crop in 1987 and a subsequent strong yearling class in 1988. Males predominate in the harvest of both of these age groups, thus increased representation of these ages in the population would tend to increase the representation of males in the harvest.

References

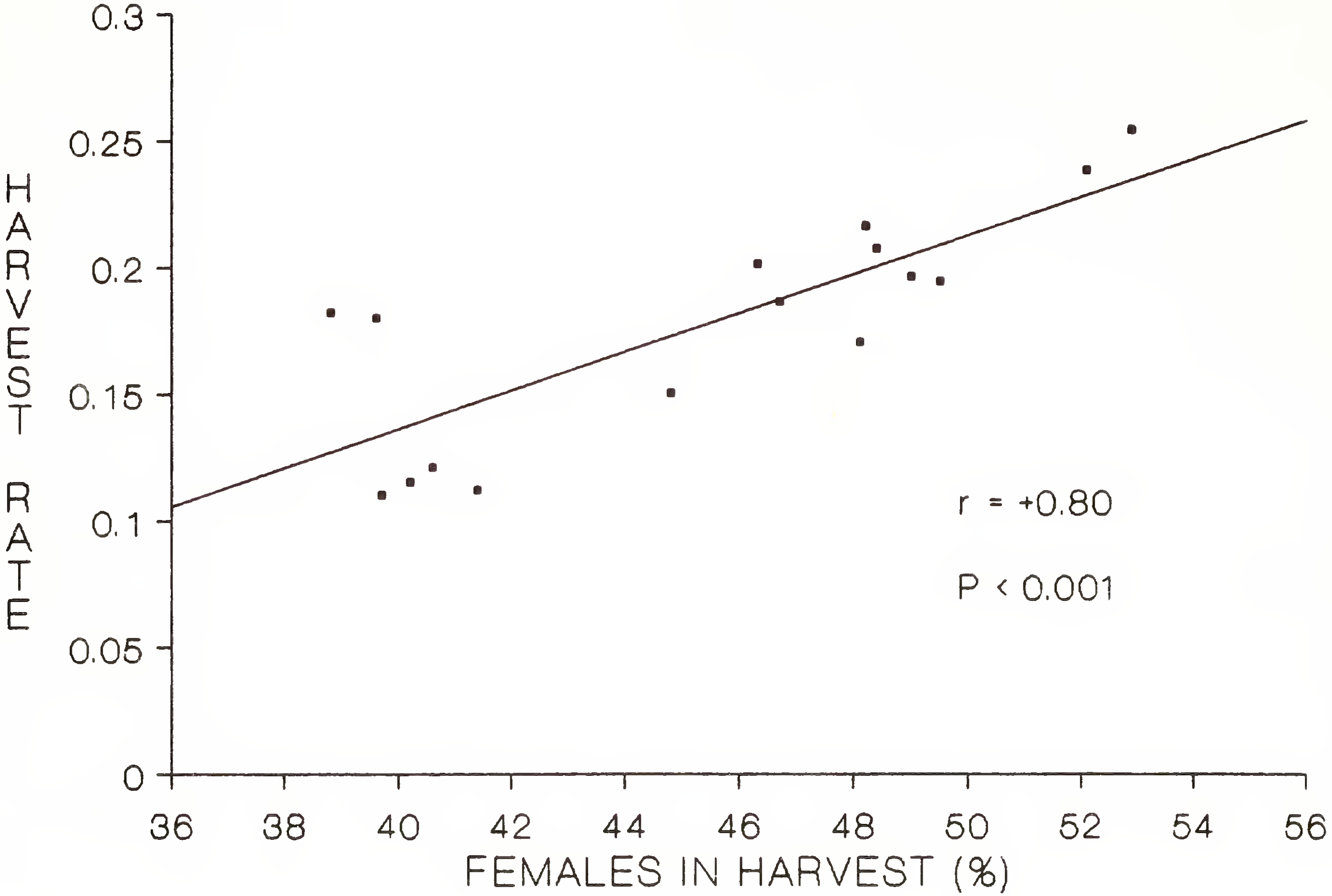
1. White and Banasiak, 1962
2. Laramie and White, 1964
3. White, 1968
4. Roseberry and Woolf, 1988

Table 10. Annual percentage of females in harvest compared with population size, population change, and harvest rates, Crab Orchard NWR, 1973-1988.

Year	Percent Females in Harvest	Population[a]		Harvest Rate	
		Size	Percent Change	Total	Females
1973	40.6	4429	-08.4	0.164	0.121
1974	46.3	3578	-19.2	0.252	0.201
1975	41.4	3690	+03.1	0.165	0.112
1976	39.7	3616	-02.0	0.166	0.110
1977	40.2	3475	-03.9	0.176	0.115
1978	46.7	3084	-11.3	0.249	0.186
1979	52.9	2661	-13.7	0.309	0.254
1980	52.1	2394	-10.0	0.279	0.238
1981	49.5	2310	-03.5	0.235	0.194
1982	48.1	2328	+00.8	0.207	0.170
1983	44.8	2375	+02.0	0.194	0.150
1984	49.0	2263	-04.7	0.231	0.196
1985	48.4	2130	-05.9	0.246	0.207
1986	48.2	2194	+03.0	0.256	0.216
1987	38.8	2003	-08.7	0.261	0.182
1988	39.6	----	--	0.265	0.180

[a] Following year.

Fig. 11. Percent females in the harvest vs. estimated female harvest rate, Crab Orchard NWR, 1973-1988.


HARVEST RATE
0.3
0.25
0.2
0.15
0.1
0.05
0
36
38
40
42
44
46
48
50
52
54
56
FEMALES IN HARVEST (%)
r = +0.80
P < 0.001

Variation B: "Hayne-Gwynn"

Description

Hayne and Gwynn (1977) proposed that herd growth could be controlled by manipulating the proportion of females in the harvest.

Assumptions

1. Rates of recruitment and natural mortality are constant.
2. Differential vulnerability and selectivity involving harvest of the sexes is constant.

Input

1. Proportion of females in the harvest.

Output

1. General indication of the likelihood of future herd increase, decline, or stability.

Test Data

The annual percentage of females in CONWR harvests (1973-1987) was compared with estimated population size and rate of change the following year (Table 10).

Results

There was a significant negative correlation ($r = -0.54$; $\underline{P} < 0.05$) with subsequent population size (Fig. 12); the correlation was stronger ($r = -0.78$; $\underline{P} < 0.001$) when 1987 was deleted. No relationship existed, however, between percent females in the harvest and population change the following year ($\underline{P} < 0.20$).

Discussion

This strategy was first developed intuitively by deer biologists in Virginia who observed that most regional herds appeared to stabilize when the percentage of females in the harvest was maintained between 30-40%. Hayne and Gwynn (1977) attempted to explain the phenomenon based on population theory and logic. They presented a simple model to demonstrate that so long as percentage females in the harvest was <50%, the relationship between doe and buck harvest rates was curvilinear, and that the lower the percentage of females in the harvest, the flatter the curve. In other words, the harvest rate of does remained relatively low regardless of how high the buck harvest rate was so long as the percentage females in the harvest was relatively low. Hayne and Gwynn (1977:118) explained how this related to the Virginia harvest strategy: ". . . the practice [of maintaining a low percentage of females in the total harvest] established a 'quota' for a number of antlered bucks that must be removed before another antlerless deer may be taken. If this quota is set high enough, then relatively few anterless and fewer females, can be taken under even the most extreme hunting pressure [because] . . . the number of antlered deer will be reduced and it will be increasingly difficult to harvest the quota."

In the Discussion following Hayne and Gwynn's paper, Downing (1977) argued that percentage does in the harvest indicated nothing about whether a herd was increasing or declining; rather, it was numbers harvested that counts. Hayne (1977) agreed that the percentage itself was not the ultimate factor, but, he argued, by keeping the percentage below a particular level, the number of does killed would automatically be kept down. He stated (p 124): ". . . we are not talking about the herd arriving itself at a percentage female in the kill - we are talking about manipulating percentage female in the kill by using regulations."

Downing (1981) later acknowledged that as a quota system, keeping percent females in the harvest low would reduce their numerical kill. However, he remained skeptical of the system as a management tool. Downing used a simple model to show how percent females can change or remain stable as various other parameters change. He also argued that the "correct" percent females (to achieve stability) could be found only by trial and error because knowledge of other herd parameters necessary to derive it theoretically would be lacking in most cases. He further noted that most agencies using the technique took the easy way out by selecting a percentage that appeared to work somewhere else.

Euler and Smith (1985) evaluated the Hayne-Gwynn approach using the model ONEPOP. They concluded: "Clearly, a technique for developing and evaluating harvest quotas from harvest data only is relatively simplistic. However, for a manager faced with the everyday reality of inadequate data, this technique provides another tool . . . Even though a system using quotas based on harvest sex ratios cannot indicate how much or how fast a herd will decline or grow, it can ensure the manager that the probability of a decline due to hunting is minimal."

References

1. Hayne and Gwynn, 1977 (original)

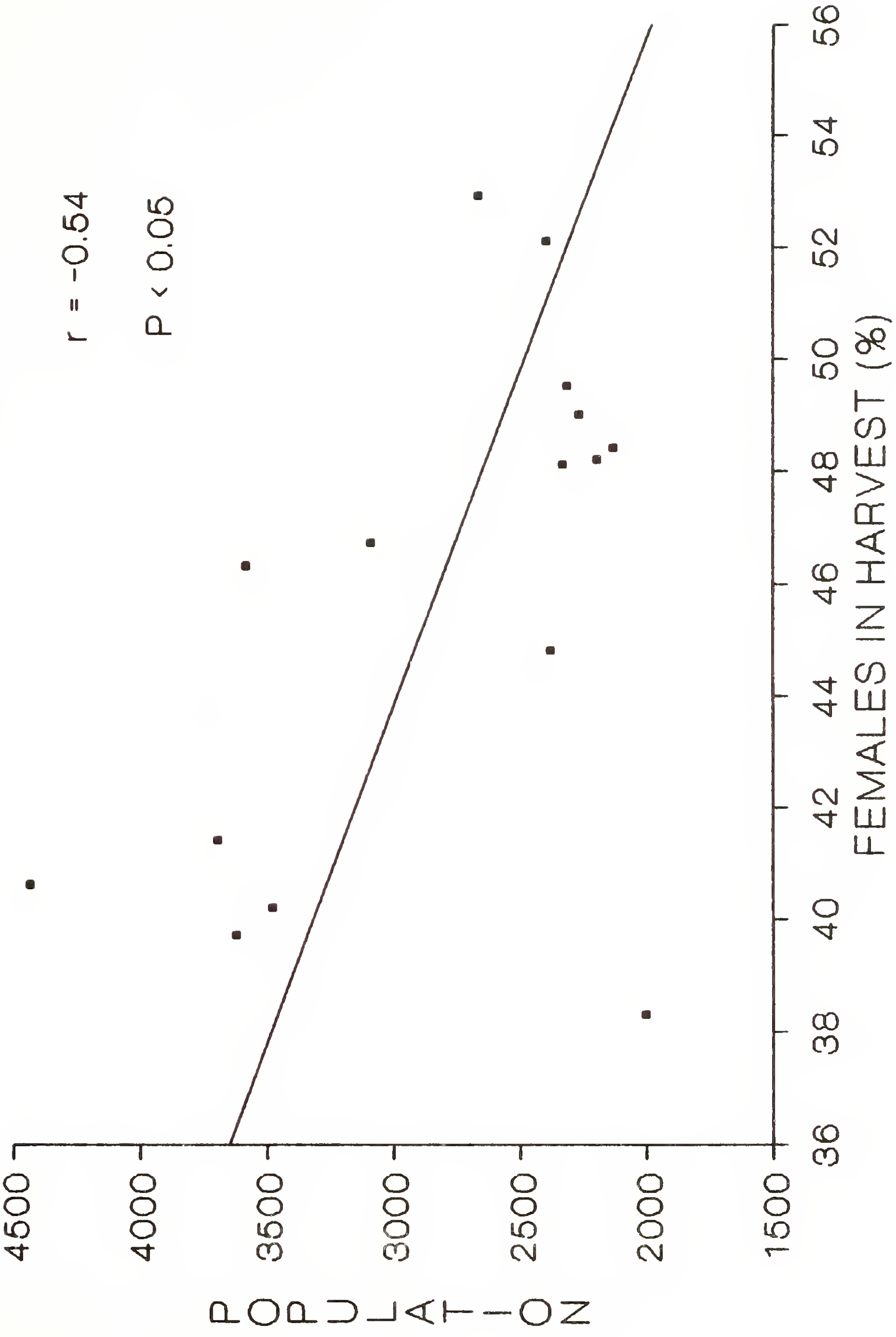
2 Downing, 1977 (Discussion following above paper)

3. Hayne, 1977 (Discussion following above paper)

4. Downing, 1981 (critique)

5. Euler and Smith, 1985 (evaluation)

Fig. 12. Percent females in the harvest vs. model population, Crab Orchard NWR, 1973-1988.


r = -0.54
P < 0.05
POPULATION
4500
4000
3500
3000
2500
2000
1500
36
38
40
42
44
46
48
50
52
54
56
FEMALES IN HARVEST (%)

Variation C: "Dickinson"

Description

Dickinson (1982) proposed a method of achieving population stability by maintaining an adult female:adult male ratio in the harvest equal to the corresponding sex ratio at the time of recruitment into the adult population.

Assumptions

1. Legal harvest is the most important cause of mortality, *or* the proportion of total losses attributable to hunting is the same for both sexes.
2. Harvested deer represent a random sample of the prehunt population.

Input

1. Proportion of females in the harvest.
2. Knowledge of sex ratio at recruitment.

Output

1. A tool for stabilizing population growth.

Test Data

This method was tested via simulations using the CONWR population model.

Results

Given a situation in which the proportion of total losses attributable to hunting was the same for both sexes, the simulated population stabilized when the sex ratio of the harvest equaled the sex ratio at recruitment.

Discussion

According to Dickinson (1982:76): ". . . a ratio of adult females to adult males in the legal harvest that is equal to the corresponding sex ratio for deer at the time they are recruited into the adult (1 year olds and older) population will produce stabilization regardless of the number or percentage of adult males removed or the ratio of fawns to adult females in the harvest or the rate of reproduction." The preceding is true given the assumptions listed above; however, Dickinson failed to make clear that the *level* at which stabilization occurs depends on the prevailing rate of recruitment. Dickinson (1982) concluded that trial and error would be necessary to select the target sex ratio for a particular area because of unknowns involving natural mortality. In essence, his approach is equivalent to Variation B where the "correct" percent females in the harvest must be determined empirically.

Underwood and Porter (1985:94) evaluated the above technique and concluded: "Harvest sex-ratio-based models can be useful management tools if applied correctly. In nearly all instances [however], ratios are *meaningless* unless they translate to numbers of deer harvested relative to the number in the prehunt population."

References

1. Dickinson, 1982 (original)
2. Underwood and Porter, 1985 (evaluation)

Technique VIII: Lang and Wood's "Pennsylvania" Method

Description

Lang and Wood (1976) described a step-by-step method for utilizing harvest data to estimate current population size and predict prehunt abundance the following year. The procedure, which is similar to one described earlier by Severinghaus (1969), is as follows:

1. The "average annual reduction rate" (AARR) for adult males is computed from the male harvest age structure as:

   $$\text{AAAR} = \frac{1.5 - 3.5}{1.5 + 2.5 + 3.5}$$

2. Adult male harvest is divided by AARR to obtain prehunt adult male population.
3. Adult female:adult male ratio (FA:MA) is computed using Severinghaus and Maguire's (1955) technique:

   $$\text{FA:MA} = \frac{\text{\% yearling males in buck harvest}}{\text{\% yearling females in doe harvest}}$$

   This adult sex ratio is then multiplied by the female fetus:male fetus ratio to adjust for possible unequal recruitment into yearling class. However, Lang and Wood assume this fetal ratio to be 1:1 so in effect there is no adjustment.
4. Prehunt adult male population is multiplied by FA:MA to obtain prehunt adult female population.
5. Male fawn:adult female and female fawn:adult female harvest ratios are obtained from antlerless harvest and summed to give recruitment rate.
6. Recruitment rate is then multiplied by estimated prehunt adult female population to give fawn crop. Fawns added to prehunt adult

females to give prehunt antlerless population. Antlerless and adult male estimates then summed to give total prehunt population.

The following procedure is used to predict next year's population and set quotas:

1. Prehunt population for bucks, does, and fawns for Year 1 are estimated using the above method.
2. Posthunt population for these classes are derived by subtracting the known harvest from prehunt estimates.
3. Recruitment into Year 2 is estimated based on posthunt doe population and previous fawn:doe ratios.
4. Prehunt population for Year 2 is obtained by adding recruitment to the posthunt population.
5. Antlered buck harvest in Year 2 is predicted from prehunt population and recent harvest rates.
6. Antlered harvest estimate subtracted from estimated recruitment to derive necessary antlerless harvest such that total harvest equals recruitment (to stabilize herd).
7. Number of antlerless permits to issue derived by multiplying desired antlerless harvest by past 3-year mean success rate.
8. Antlerless harvest in Year 2 predicted from the number of permits to be issued and the previous 3-year mean success rate.
9. Observed antlerless harvest compared with expected.

Assumptions

1. Total antlered male harvest is known or can be estimated.
2. Adult sex ratio and fawn:doe ratio based on harvest data are accurate reflections of actual herd conditions.

Input

1. Annual harvest data by sex/age class at least thru age 3.5.

Output

1. Estimate of absolute population size.
2. Prediction of next year's prenhunt population.

Test Data

The above method was run with 1973-1988 CONWR harvest data as input. Several alternative ways of calculating parameters were also tested; these were:

a) AARR computed according to Severinghaus (1969) or Downing (1980), i.e.,

$$\frac{1.5}{1.5 + 2.5 + 3.5+} \quad \text{or} \quad 1 - \frac{2.5 + 3.5+}{1.5 + 2.5 + 3.5+}$$

b) FA:MA ratio adjusted according to Creed et al. (1984), i.e., divide the proportion of yearlings in the adult male harvest by the male/female fawn harvest ratio.

c) FA:MA obtained from July-August roadside observations.

d) Recruitment rates based on CONWR studies of reproductive and fawn survival studies rather than from harvest data.

Results.--The above produced 12 variations of the basic Lang-Wood method. However, because recruitment rates based on CONWR field studies were almost identical to harvest data (0.936:1 vs 0.940:1), only runs using the latter were reported (Table 11). Downing's (1980) alternative method of computing AARR produced population estimates that averaged 17% lower than the original Lang-Wood method (range -47 to -3%). Estimates using Creed et al's (1984) adjustment of FA:MA averaged 13% below the standard (range -32 to +8%) whereas estimates using census data averaged 28% above (range -1 to +69%).

The 6 variations were compared by computing the square root of the sum of each method's annual deviations from the model. Using this approach, AAA performed best during the period 1975-1988 while ACA was best during 1973-1988. Annual population estimates from alternative AAA (Lang and Wood's original version) averaged 18.6% below those of the model (range -53 to +18%). Adding estimated male crippling losses (11.8%) to the male harvest produced estimates that averaged 8.9% below the model. All alternatives, however, tended to produce rather erratic annual estimates that did not tract the real population particularly well (Fig. 13).

Discussion

Fluctuations in year-to-year estimates appeared to be more realistic for regional Illinois data set (presented later) than for CONWR. This was due to primarily to greater stability in the AARR statistic owing to larger regional sample sizes. The tendency for annual population levels on CONWR to be underestimated is more difficult to explain. As noted previously, harvest data appeared to give relatively unbiased estimates of fawn:doe and FA:MA ratios. Furthermore, the acknowledged negative bias of AARR would act to overestimate population size rather than underestimate it (Downing 1980). The problem may come from using only recorded male harvest with AARR (the estimated mortality rate from all causes) to derive prehunt abundance. A higher (and more accurate) estimate would be obtained if the numerator included all annual losses (harvest, crippling, and natural).

Lang and Wood (1976) implied that comparisons of actual and predicted antlerless harvest was an indication of the accuracy of their method. We disagree. The predicted harvest for a particular year is based on the number of permits to be issued and the past 3-year average success rate, whereas the observed harvest is a function of that same number of permits and the actual hunter success. Therefore, the only thing being compared is the success rate for a given year and the average success rate for the previous 3 years.

Reference

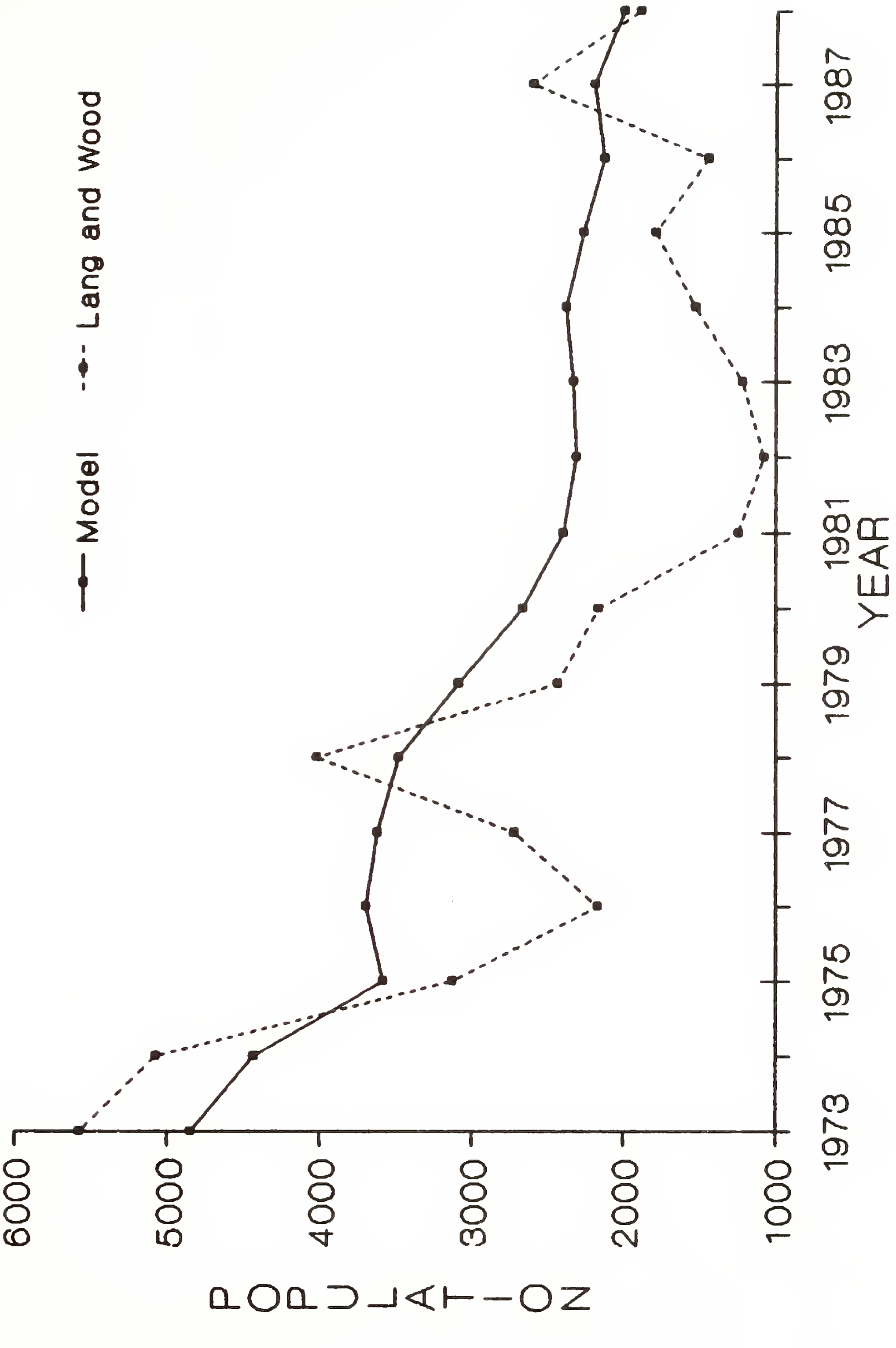
1. Lang and Wood, 1976 (original)

Table 11. Lang and Wood population estimates with variations, Crab Orchard NWR, 1973-1988.

Year	Variations[a]					
	AAA	ABA	ACA	BAA	BBA	BCA
1973	5576	4620	7424	2975	2465	3961
1974	5070	4589	8441	3255	2946	5419
1975	3126	2654	3093	2230	1894	2207
1976	2168	1644	3349	1737	1317	2683
1977	2718	2482	3477	2052	1874	2626
1978	4015	3103	5417	3109	2403	4195
1979	2431	2566	2887	2236	2361	2656
1980	2163	2336	2609	1955	2112	2359
1981	1248	1011	1466	1190	963	1397
1982	1080	921	1294	1016	866	1217
1983	1221	1050	1639	1122	965	1508
1984	1527	1363	2436	1308	1167	2086
1985	1790	1474	2236	1539	1267	1922
1986	1447	1358	1772	1400	1315	1716
1987	2597	1753	3265	2196	1482	2760
1988	1894	1572	2693	1661	1379	2363

[a] AARR: A = Lang & Wood; B = Downing.
FA:MA A = Lang & Wood; B = Creed; C = census.
F:D A = Lang & Wood.

Fig. 13. Lang and Wood population estimates and model population, Crab Orchard NWR, 1973-1988.


POPULATION
6000
5000
4000
3000
2000
1000
1973
1975
1977
1979
1981
1983
1985
1987
YEAR
Model
Lang and Wood

Technique IX: Fraser

Description:

Fraser (1976) initially described a technique for estimating harvest rates of moose based on differential harvest of the sexes. The rationale is that if males are harvested at a higher rate than females, the male:female ratio will decline with age. The rate of this decline can be used to estimate overall harvest rate and differential vulnerability between the sexes (Fraser et al. 1982). If the sexes enter the age of initial differential harvest in equal numbers, and if harvest effort is constant over time, the percent of the population removed annually is approximately 1/age at which percent males declines to 50. If hunting effort is not constant, then the log of the male:female ratio for each age class can be regressed on the cumulative hunting effort during the life of that cohort using a weighted, non-linear, least squares procedure (e.g. PROC NLIN; SAS, 1982). The 2 parameters ($\underline{p}$ and $\underline{u}$) obtained from this regression can be combined to provide instantaneous harvest rate estimates for males and females. For a complete description of this procedure including calculation of cumulative effort, see Paloheimo and Fraser (1981).

Assumptions

1. There is differential harvest of males and females beginning at a certain age.
2. The sex ratio entering that age is even.
3. Non-hunting mortality is the same for males and females.
4. The proportion of the population taken per unit of hunting effort is constant.

Input

1. Harvest data by sex-age class.
2. Estimate of annual hunting effort.

Output

1. Estimate of annual harvest rates for adult males and females.
2. Estimate of absolute prehunt adult population size (if total harvest is known).

Test Data

Harvest sex-age structure and annual number of hunters during 1975-1988 CONWR hunts were used as input data.

Results

Estimates of adult population size averaged 35% below those indicated by the model, although they tracked suspected trends reasonably well (Fig. 14).

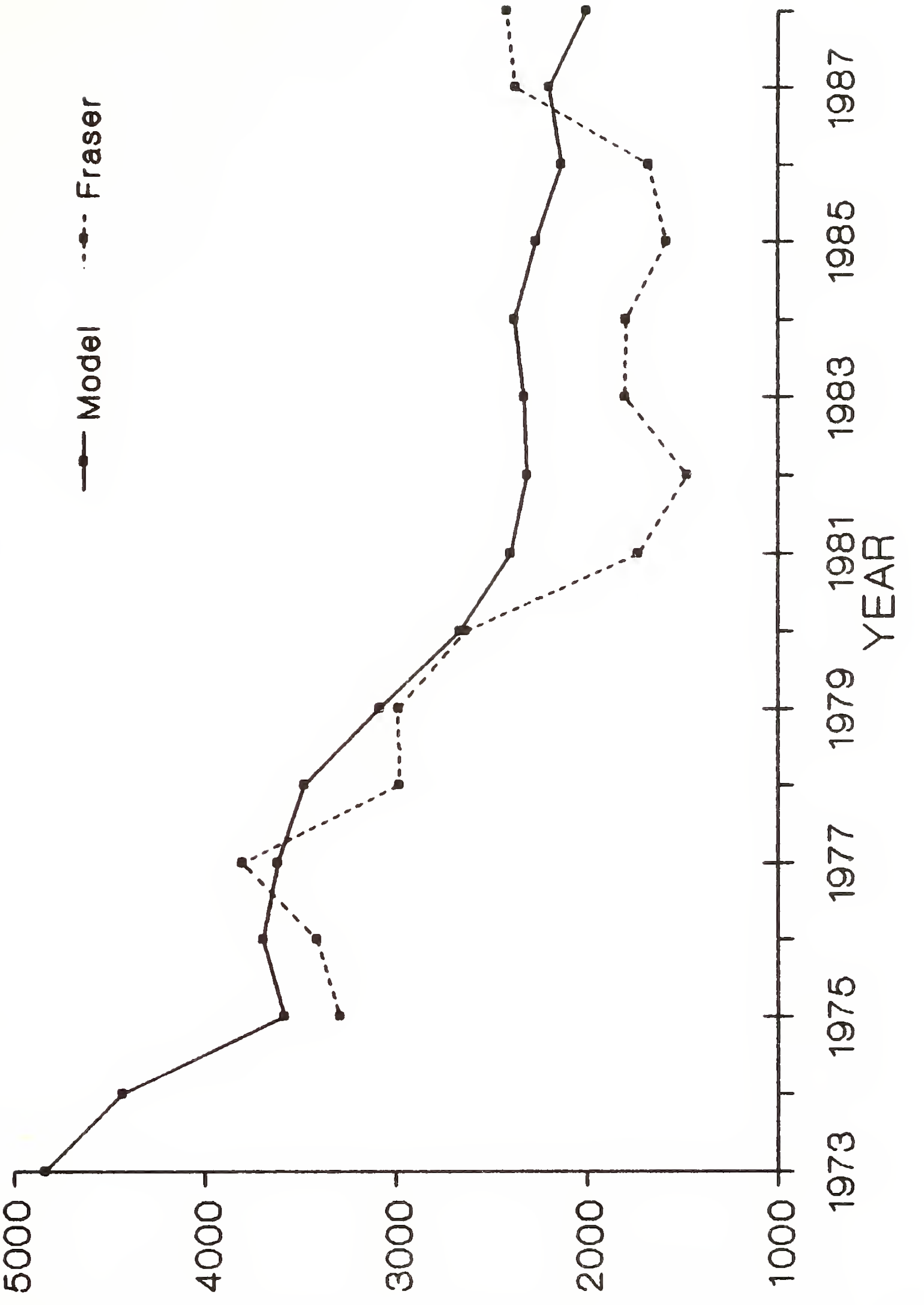
Discussion

Two assumption violations are suspected of resulting in overestimated harvest rates and thus underestimated population levels. These are unequal natural mortality rates (higher for males), and overrepresentation of yearling males in the harvest. Harris and Metzgar (1987) provide a more complete discussion of the implications of assumption violations for this technique.

References

1. Fraser, 1976 (original)
2. Paloheimo and Fraser, 1981 (description, application)
3. Fraser et al., 1982 (description)
4. Harris and Metzgar, 1987 (evaluation)

Fig. 14. Fraser population estimates (adults only) and model adult population, Crab Orchard NWR, 1975-1988.


POPULATION
5000
4000
3000
2000
1000
YEAR
1973
1975
1977
1979
1981
1983
1985
1987
Model
Fraser

APPLICATION TO REGIONAL ILLINOIS DEER HERDS

Several of the techniques described in the previous section were not applicable statewide or regionally due to lack of necessary data. These were primarily methods requiring supplemental observations in addition to harvest data (e.g. Index-Removal, CIR). The Leslie Catch/Unit Effort method could not be applied because daily effort data were not available. Two other techniques, CIR Variation C (Shope) and Fraser proved generally unsatisfactory and are not reported in detail. The Shope technique, in particular, gave erratic results, often because the computed proportion of males was higher posthunt than prehunt, thus causing the method to fail. The Fraser method indicated a general upward trend in deer numbers over the past 25 years, but unrealistic estimates occurred during those years when males predominated in all age classes.

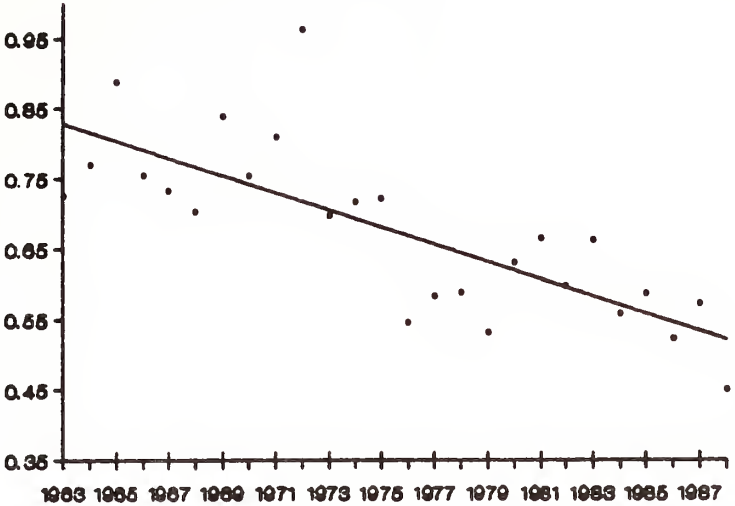
The remaining methods (standard Reconstruction, DeLury's Catch/Unit Effort, and Lang-Wood) were applied to 1963-1988 harvest data from Regions 1, 3, 4, 7, and 8 (Figs. 15-19). Also plotted were corresponding indices of sex/age composition including percent yearlings in the male harvest, primary age ratio of females, and percent females in the harvest. It should be noted that only the Lang-Wood method gives an absolute population estimate (which averaged 19% too low on CONWR). DeLury and Reconstruction estimates depend on arbitrarily selected of values for $\underline{q}$ (proportion of the population harvested per 1 unit of effort) in the case of the former, and lifetime recovery rates for males and females in the case of the latter.

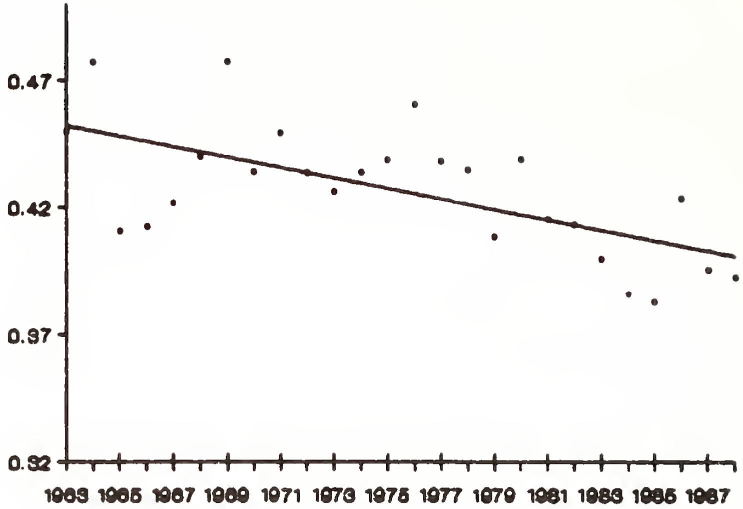
The 3 methods utilized all indicated similar long-term regional trends, i.e., relatively stability in the 1960, followed by a gradual rise through

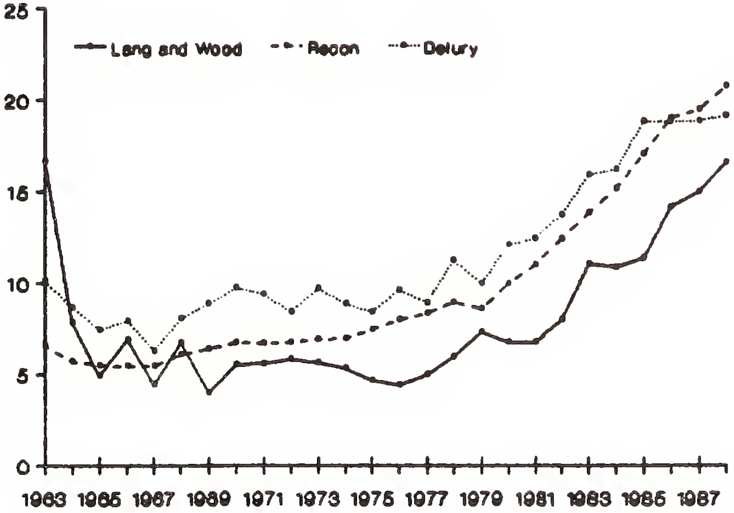
Fig. 15-19. Regional data from Illinois firearm deer seasons, 1963-1988 (clockwise from upper left: female fawn:doe ratio, percent females in harvest, percent yearlings in male harvest, population trends).

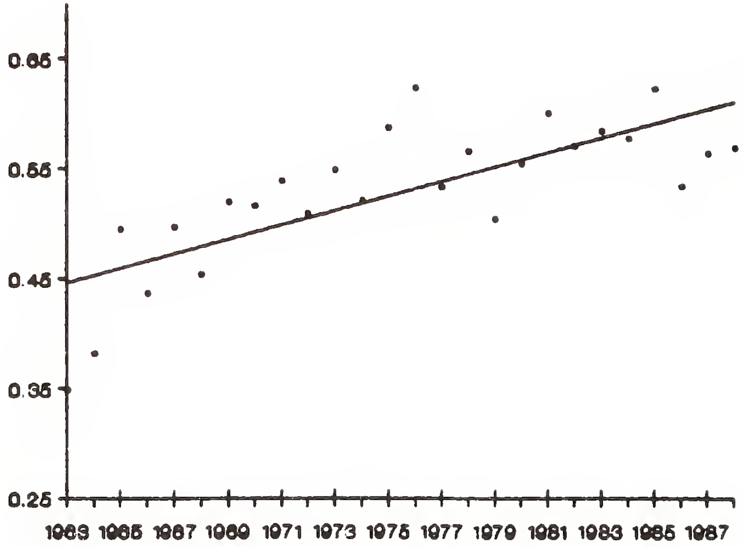
the 1970's and a more rapid increase in the 1980's. Trends in sex/age data were also similar across regions. There was an increase in the proportion of yearlings in the adult male harvest throughout the period ($P < 0.01$), apparently reflecting a general increase in male harvest rates (Burgoyne 1981). In contrast, representation of females in the total harvest declined in Regions 1, 7, and 8 ($P < 0.01$), suggesting a drop in the harvest rate for this segment of the population. This index was relatively stable over time in Regions 3 and 4, indicating that even though there has been an increase in male harvest rates, the harvest rate of females has apparently not increased. Finally, the primary sex ratio among females (fawns:adults) declined ($P < 0.01$) in all regions except 4 ($P = 0.12$). As noted earlier, changes in female age structure reflect changes in recruitment rather than mortality. Hence, this decline in the female fawns:doe ratio is interpreted as a density-dependent response to rising population levels.

REGION 1

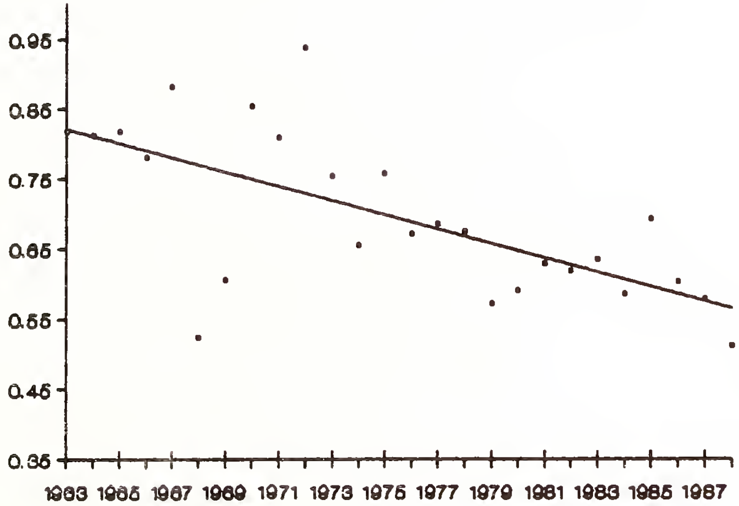

0.95
0.85
0.75
0.65
0.55
0.45
0.35
1963 1965 1967 1969 1971 1973 1975 1977 1979 1981 1983 1985 1987

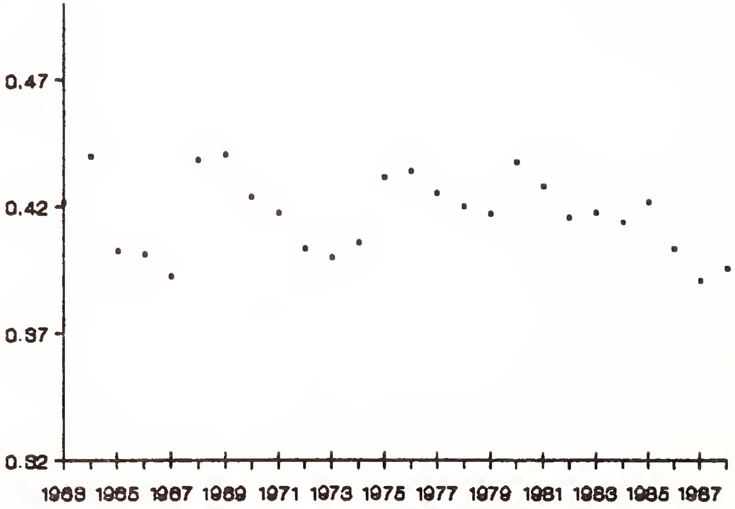

0.47
0.42
0.37
0.32
1963 1965 1967 1969 1971 1973 1975 1977 1979 1981 1983 1985 1987


25
20
15
10
5
0
Lang and Wood
Recon
Delury
1963 1965 1967 1969 1971 1973 1975 1977 1979 1981 1983 1985 1987


0.65
0.55
0.45
0.35
0.25
1963 1965 1967 1969 1971 1973 1975 1977 1979 1981 1983 1985 1987

REGION 3


0.95
0.85
0.75
0.65
0.55
0.45
0.35
1963 1965 1967 1969 1971 1973 1975 1977 1979 1981 1983 1985 1987


0.47
0.42
0.37
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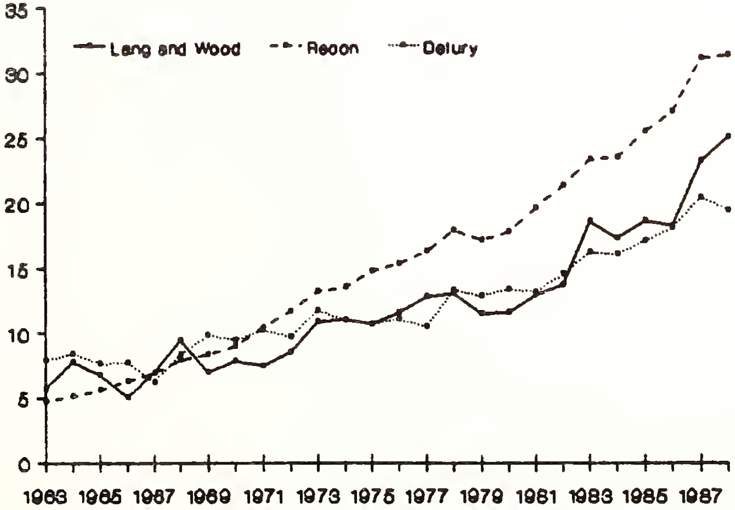
1963 1965 1967 1969 1971 1973 1975 1977 1979 1981 1983 1985 1987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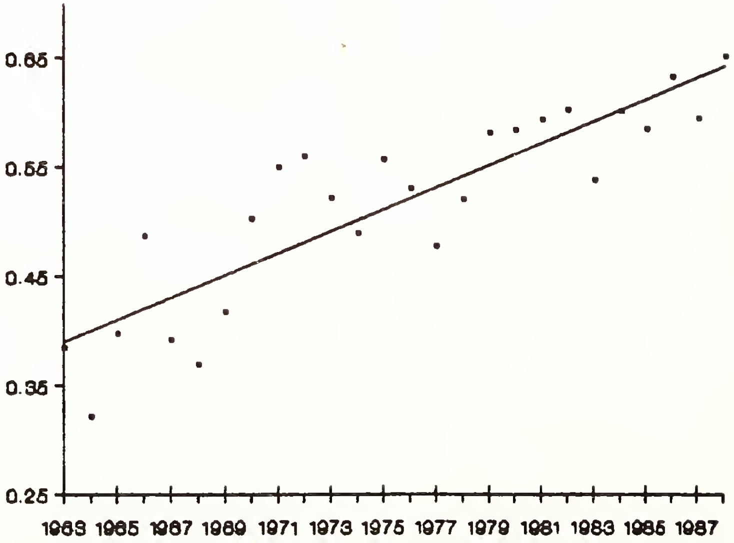
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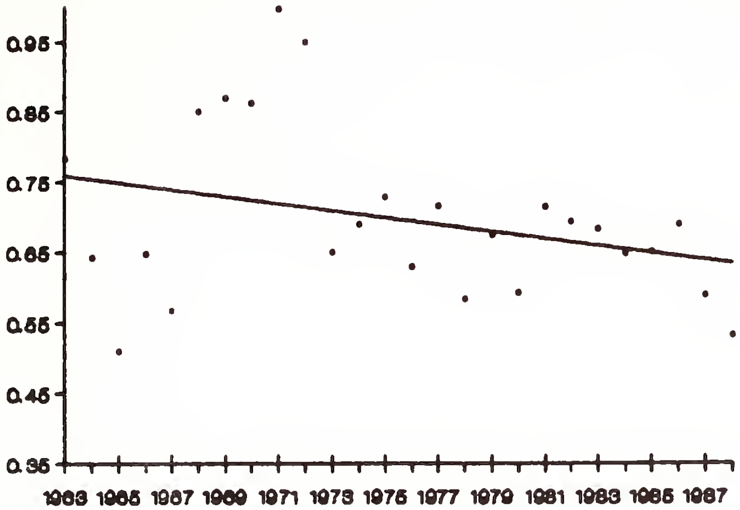
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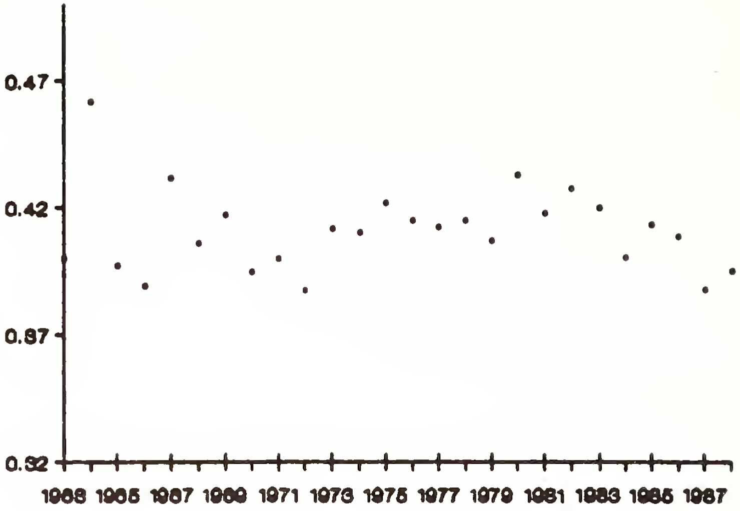
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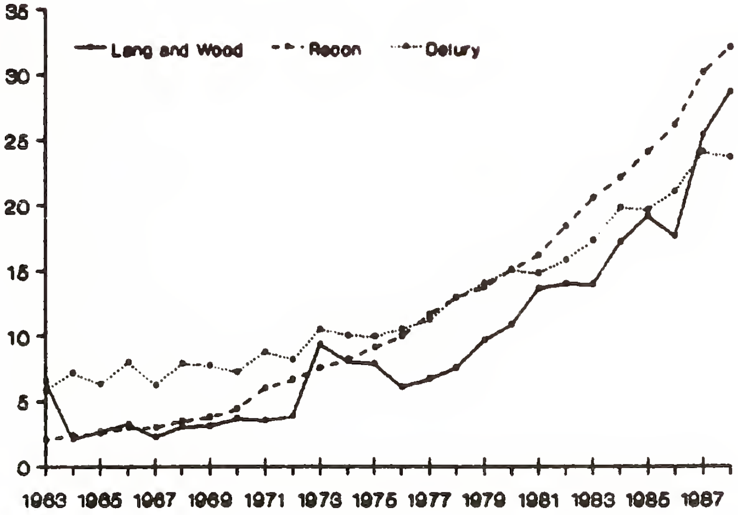
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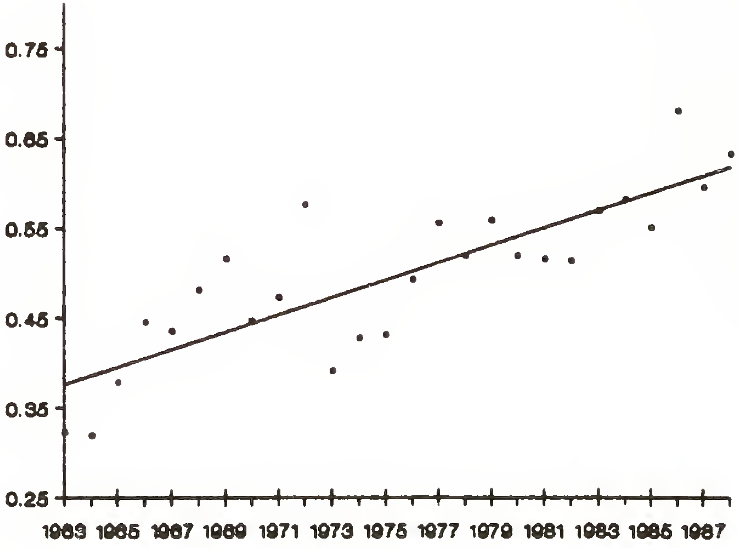
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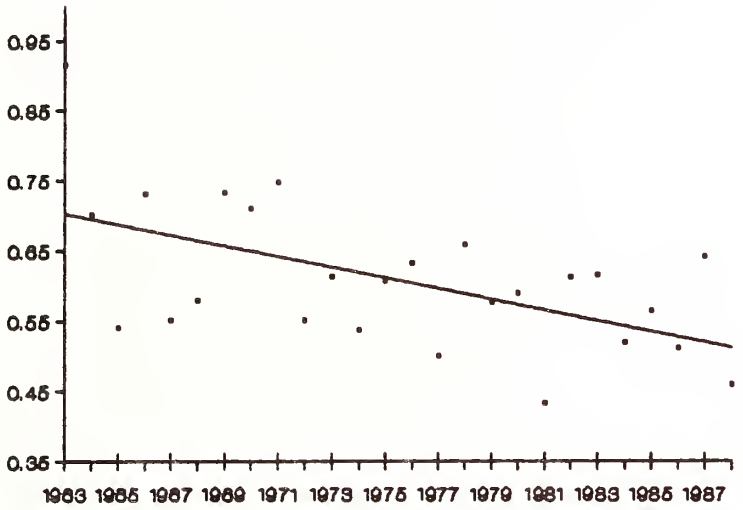
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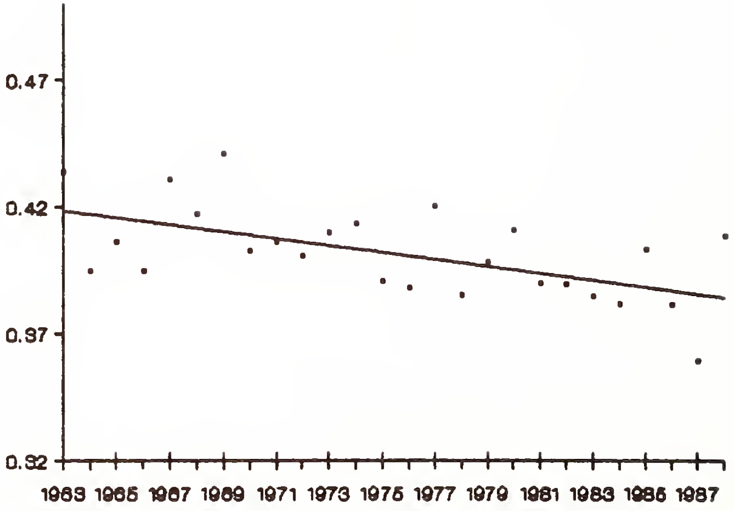
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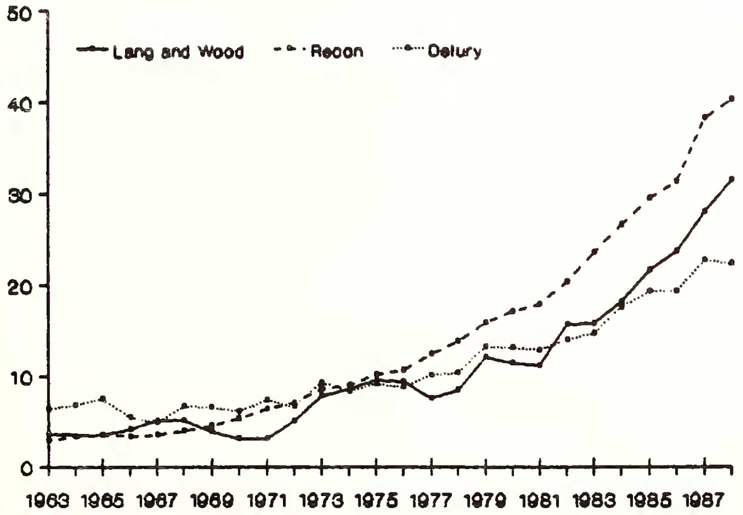
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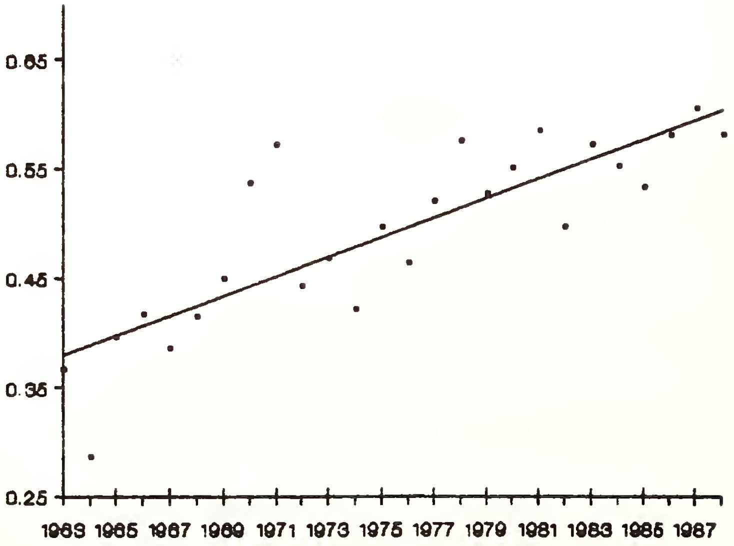
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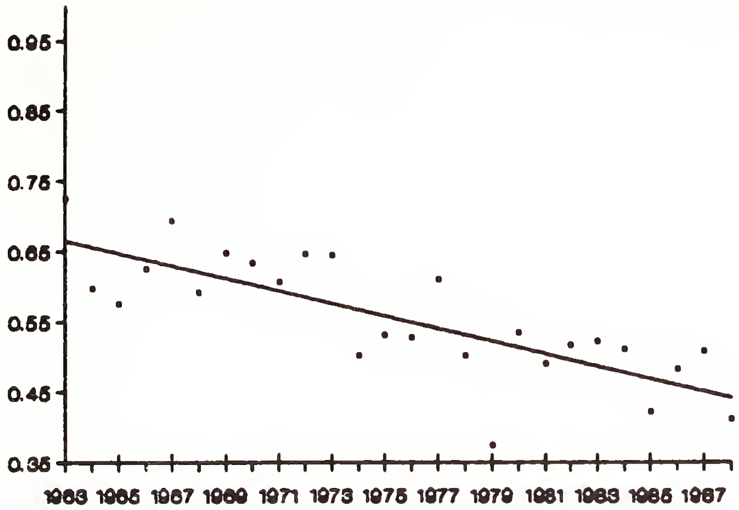
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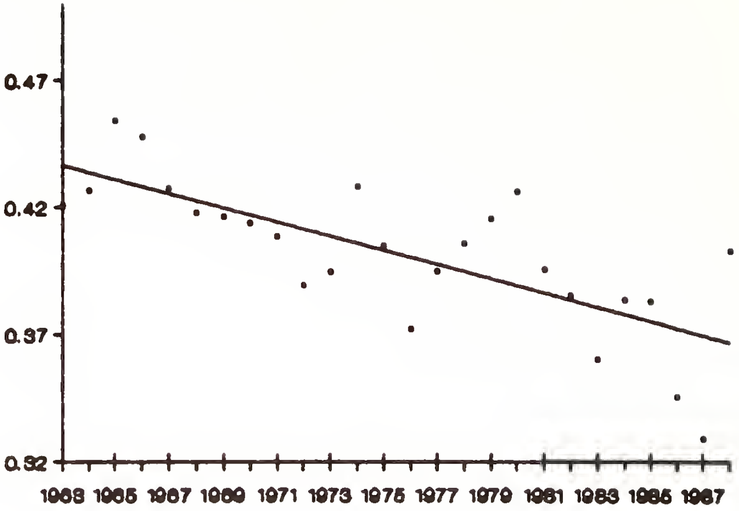
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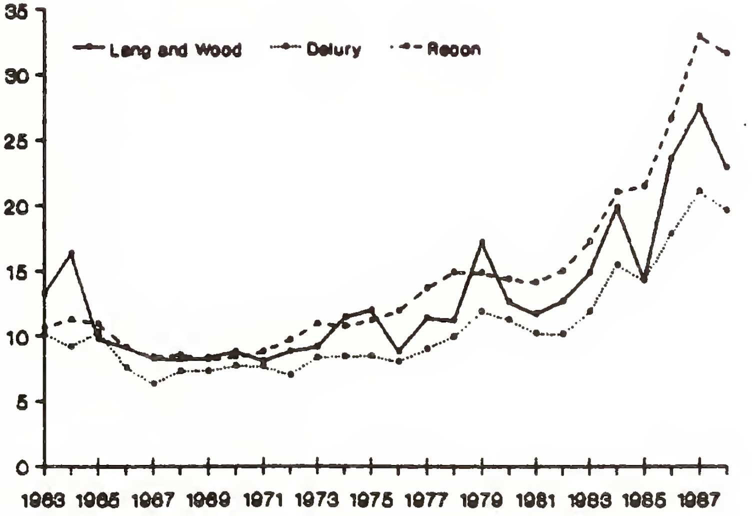
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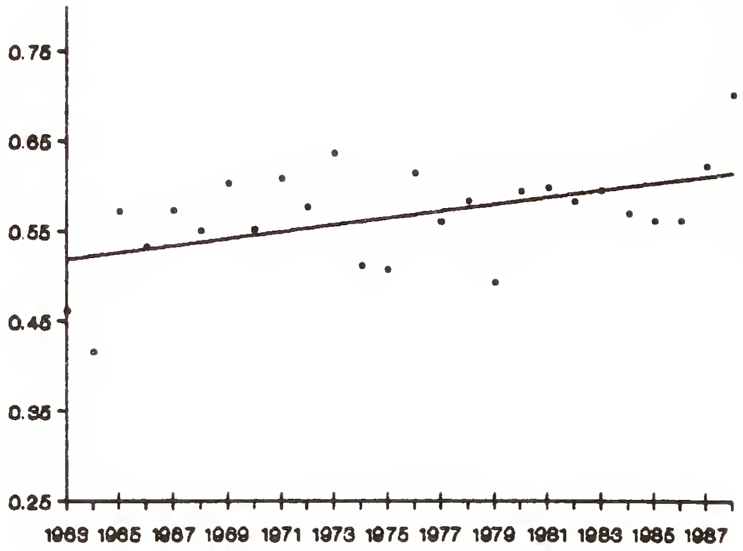
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DISCUSSION

A variety of herd-monitoring techniques and variations thereof were tested in the previous section using harvest and other data from Crab Orchard NWR. A comparative evaluation of these methods with respect to type of information provided, data required, and overall performance is summarized below. Attributes considered are defined as follows:

Accuracy: How close a particular estimate comes to the true value.

Precision: The variability or "scatter" of individual estimates or indices regardless of their accuracy.

Sensitivity: The ability to detect change of a given magnitude.

Robustness: Relative tolerance to biased input and/or violation of assumptions.

Output Produced

Products of the various techniques can be categorized as to type of information provided (abundance, parameters, both); type of estimate (absolute, relative); and timeframe (retrospective, predictive). Absolute estimates of population size are given by the Index-Removal method, several of the Catch/Unit Effort techniques, CIR, Lang-Wood, and the Fraser method (adults only). The DeLury (Variation D) Catch/Unit Effort and Reconstruction methods provide absolute population estimates only when certain parameters are assigned a value (proportion of the population taken by 1 unit of effort for the former; lifetime recovery rates for the latter). Rarely would these be known with certainty; hence the 2 techniques generally provide only indices of relative abundance rather than estimates of absolute population size.

Most of the techniques give only retrospective assessments of population performance. The extreme being Reconstruction which, by necessity, has a lag of at least 3 years unless used in combination with other techniques. Those which predict subsequent population size include CIR Variation C and D, and Lang-Wood. Variation B and C of the Harvest Sex Ratio approach also imply predictive capabilities in that they purportedly offer a means of controlling population growth.

Accuracy

Accuracy requirements in a given situation depend on the purpose of the estimates. If relatively little is known about a particular herd or area, then population estimates within 20-30% might be of some value. On the other hand, this level of accuracy would not be adequate for setting harvest quotas. None of the methods tested which provided estimates of absolute abundance were particularly accurate. Mean population estimates from Lang-Wood, Fraser, CIR Variation C, and Index-Removal ranged from 18.6 to 35.0% too low while CIR Variation A averaged 16.6% too high.

Precision

Subjectively, it appeared that standard Reconstruction and the DeLury Catch/Unit Effort method gave the most stable (precise) estimates over the period of relative population stability on CONWR (1981-1988). Annual estimates from the Lang-Wood and Fraser techniques showed considerably more variation over this period, while those from all CIR variations and the Index-Removal method were quite erratic. Precision of the Reconstruction and DeLury methods were comparable during the period of relative population stability but not during periods of change. Reconstruction tended to underestimate population size early in the study when harvest rates were low and overestimate abundance during the population decline of 1977-1981 which resulted from an increase in harvest intensity.

A more quantitative measure of precision was obtained by comparing the variance of various estimates of male mortality/harvest rates. Such estimates were available from Reconstruction, CIR Variations B and C, Lang-Wood, Fraser, and Harvest Age Ratios Variation A. Mean annual estimates from these various sources were relatively similar (range .53 - .65), but variance differed substantially. Values from Reconstruction were most stable (CV = 12%), followed by Harvest Age Ratio Variation A (21%), and Fraser (26%). The remaining methods had CV's of 31-32%.

Precision of a particular estimator can also reflect sampling error in input data. For this reason, estimators using large data sets would be expected to give more stable, although not necessarily more accurate, results. During the period 1978-1988, CONWR annual harvests averaged 617 compared to 3100-5400 for the major Illinois Regions. Adult sex ratio calculated by the Severinghaus-Maguire method for this period showed an average CV of 10.2% on CONWR compared to 10.6 for individual regions. Lang-Wood's AARR value, however, was considerable more variable on CONWR (CV = 16.4%) than for the individual regions (CV = 10.9%).

Sensitivity

The CONWR deer herd experienced 2 major periods of population changes during the study - an approximate 25% decline from 1973 to 1975 following initiation of hunting, and a 30% decline from 1978 to 1981 resulting from intensified harvesting. All of the population monitoring techniques except CIR Variation A and Index-Removal detected the 2nd decline (1978-1981) to varying degrees, while Reconstruction, Lang-Wood, and CIR Variation A detected the 1st (DeLury and Fraser methods could not be tested during this period). Considering periods of both stability and fluctuation, we rank the techniques in the following order of sensitivity: DeLury, Reconstruction, Fraser, Lang-Wood, CIR Variation A, CIR Variation C, and Index-Removal. Reconstruction, due to its responsiveness to the numerical harvest, did not fully reflect the initial population decline on CONWR because of the numerical difference in the 1st and 2nd year's harvest totals.

Robustness

In a practical sense, robustness of a method can derive from internal stability of the method itself or from the relative stability of its input data. Virtually all of the systems tested are logically and/or theoretically sound, i.e., they produce unbiased results if input data are unbiased and assumptions are met. Unfortunately, white-tailed deer harvest and observation data often do not meet these criteria. Harvest data are chronically biased due to differential vulnerability of various sex/age classes and selectivity among hunters (Roseberry and Woolf 1988). Incorrect age determination of the harvested sample can further complicate the problem (Roseberry 1980). Observational data are often biased by differential seasonal behavior of sex/age classes (Downing et al. 1977, McCullough 1982) and this can cause serious problems in their use in population monitoring techniques (Downing 1980, Eberhardt 1982).

In general, the most robust methods were those requiring the fewest assumptions and/or simplest input datasets. Methods using ratios in their calculations, especially CIR, seemed least robust - an observation originally made by Dasmann (1952).

Data Required

The most modest data requirements were those of the Harvest Sex Ratio methods which required only an estimate of the proportion of females in the total harvest. Next were the Catch/Unit Effort methods which required an estimate of the total kill and some measure of effort expended. Somewhat more data intensive were Reconstruction, Shope's CIR, Life Tables, Harvest Age Ratios, Lang-Wood, and Fraser which all required harvest sex/age frequencies at least through age 3.5 or 4.5. The most data demanding techniques were the conventional CIR applications and the Index-Removal method which utilized observational data before and after the hunt in addition to harvest data.

RECOMMENDATIONS

Index-Removal and CIR

These methods, while theoretically sound, produced unsatisfactory results when applied to the CONWR dataset. The principal reason appeared to be seasonal differences in observability of deer unrelated to the numerical harvest. Because this is a general and not a local problem, we do not believe it worthwhile to initiate collections of pre- and posthunt observational data for the purpose of utilizing these techniques. In those situations where such data are routinely collected, we recommend caution in the use and interpretation of CIR based on the generally poor performance we encountered.

Reconstruction

This method is appealing because of its underlying simplicity and logic. Users should be aware, however, of its sensitivity to changes in the numerical harvest. If such fluctuations reflect changes in harvest intensity rather than population size, indicated trends will be biased. A second drawback is that the method provides information only for the relatively distant past. Utilizing other techniques in combination with standard Reconstruction to assess more recent years introduces additional assumptions which may be difficult to validate. For intensively-studied herds where most of the annual mortality can be accounted for, reconstruction offers a powerful tool. In situations where only harvest losses are recorded and their relative contribution to total mortality is unknown, the technique is of more limited value. Moreover, population statistics or parameters calculated from reconstructed cohorts can be seriously biased. For example, reconstructed fawn:doe ratios will generally be too high as will harvest rate estimates for individual cohorts. Despite these shortcomings, we believe that if necessary data are available, population reconstruction should be carried out so long as limitations are kept in mind. In regions with a tradition of any-deer seasons, we recommend that the entire population be reconstructed. The alternative of reconstructing only one sex or age group and projecting to the entire population using computed sex/age ratios introduces additional assumptions and sources of bias into the procedure.

Life Tables

McCullough (1979:221) noted that attempts to apply life-table analysis to harvest data have generally "not proven useful at the practical level." Based on our experience with the CONWR deer herd, we would tend to agree. Dynamic, exploited deer herds seldom have stable age distributions, a vital assumption for life table analysis. In addition, harvest data are often biased samples of the living age structure. For these reasons and others, we believe that formal life table analyses are more suited to the theoretical population ecologist than the practical game manager.

Harvest Sex/Age Ratios

As noted earlier, a good deal of controversy and confusion has surrounded the use of harvest sex and age ratios. Alone, these data do not provide sufficient information for precise management. However, we believe that certain sex/age statistics can and should be routinely monitored for the general information they do provide. Specifically, it appears that trends in the harvest rate of antlered males can be obtained by monitoring the percentage of yearlings in the antlered harvest. We also recommend monitoring the fawn:doe ratio and/or the female fawn ratio as it appears to be a general indicator of relative population size and can be used to identify "strong" cohorts in subsequent years.

Use of percent females in the harvest to establish harvest quotas or otherwise direct strategies would appear appropriate only in extreme situations where: (1) little or no other data are available, or (2) sufficient data are available to permit determination of an appropriate target percentage, either empirically or theoretically based on detailed knowledge of other herd parameters. In more typical situations, we recommend monitoring the percentage females in the harvest as a general index to relative trends in the female harvest rate.

Success Per Unit Effort

Certain variations of this approach appear to offer the deer manager a useful means of monitoring herd performance with a minimum of data. We were unable to adequately evaluate the Leslie method (Variation B) with the long-term CONWR dataset. This variation does have the advantage of providing an absolute population estimate; however, a critical assumption (i.e., no seasonal change in susceptibility to harvest) may be violated during most deer hunts. The DeLury method requires only that this remain constant from year to year, a less rigorous assumption. We recommend that this latter method be employed whenever sufficient data are available as it appears to provide a relatively consistent, sensitive index to population trends over a wide range of densities. Furthermore, if an independent estimate of population size is available, then it is possible to calibrate this technique so as to provide annual estimates of absolute abundance.

Lang-Wood and Fraser

Based on our evaluations, these methods appear to be less sensitive, precise, and robust than the DeLury Success/Effort method or Reconstruction. We do not discourage use of either of these 2 techniques as supplemental methods of data analysis; however, managers should be aware of their potential limitations and exercise appropriate care in their application and interpretation.

Data for Management

We noted in a previous paper (Roseberry and Woolf 1988:1) that: "Harvest data constitute an important source of information for the deer manager, but interpretation can be complicated by reporting bias, hunter selectivity, differential vulnerability, and aging errors." The present report emphasizes the potentially serious consequences of some of these biases in terms of correctly interpreting herd performance based on harvest data. Therefore, we strongly recommend that agencies address the 2 sources of bias over which they have some control, viz. reporting bias and aging errors. The former, which often involves underreporting of females and/or young animals when compliance is voluntary (Burgoyne 1981), can be minimized or eliminated by requiring mandatory reporting of all harvested deer. The latter problem, i.e. aging errors, can be minimized by utilizing trained professionals at check stations (Roseberry 1980).

The type and amount of data collected during annual harvests generally reflects a compromise between management needs and budgetary and manpower constraints. In the case of white-tailed deer, however, administrators should recognize that annual hunter harvests often provide virtually all of the information available to the manager, and that much of this information would be extremely difficult and expensive to obtain by conventional field or laboratory research. At the very minimum, we believe that annual data collections should include: 1) a valid estimate of the total harvest, 2) an estimate of total effort expended, 3) sex ratio of the harvest, 4) sex-specific age structure of the harvest (minimally fawn, yearling, adult; preferably by individual age class at least to 4.5+ years). We further recommend that the manager utilize this information in a variety of techniques described in this report, rather than relying a single approach to herd monitoring.

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APPENDIX A. Controlled deer harvests, Crab Orchard NWR, 1973-1988.

Year	Permits Issued	Hunters	Hours	Deer Sightings	Deer Harvested
1973[a]	---	---	---	---	795
1974[a]	---	---	4222	30874	1115
1975	800	722	3633	13767	582
1976	800	718	3821	14635	612
1977	800	716	3798	21489	635
1978	1200	1097	6286	27732	865
1979	1300	1222	7114	22191	932
1980	1200	1109	6617	10475	743
1981	1100	1017	4569	6530	562
1982	1000	922	4010	4504	478
1983	900	824	3367	4548	451
1984	1000	919	3632	5244	549
1985	1080	992	4823	5012	556
1986	1152	1043	4586	4655	546
1987	1125	995	4241	4808	572
1988	1150	1033	4323	4772	530

[a] Permits issued daily.

APPENDIX B. Annual white-tailed deer harvest by sex/age class, Crab Orchard NWR, 1973-1988.

	Males					Females					
Year	0.5	1.5	2.5	3.5	4.5+	0.5	1.5	2.5	3.5	4.5+	Total
1973	109	133	107	72	51	81	79	65	64	34	795
1974	156	184	145	76	38	134	136	150	68	28	1115
1975	86	123	86	38	8	69	49	67	36	20	582
1976	106	151	72	33	6	72	72	64	22	14	612
1977	77	171	72	47	12	68	67	75	27	19	635
1978	144	160	107	40	10	103	70	116	50	65	865
1979	129	213	62	24	11	138	108	89	63	95	932
1980	110	156	53	23	14	121	78	64	53	71	743
1981	101	144	29	9	3	77	70	60	38	31	562
1982	92	118	31	7	0	75	62	43	33	17	478
1983	74	134	20	15	6	61	54	42	22	23	451
1984	84	120	42	23	11	72	70	56	32	39	549
1985	113	116	26	22	10	89	52	62	37	29	556
1986	95	147	24	10	7	88	58	58	32	27	546
1987	125	150	44	26	5	77	42	52	30	21	572
1988	85	168	35	25	7	67	52	50	25	16	530
Total	1686	2388	955	490	199	1392	1119	1113	632	549	10523

APPENDIX C. Results from systematic roadside observations of white-tailed deer, Crab Orchard NWR, 1966-1988.

	September-November				January- February		
Year	N	Antler/ Antlerless	Fawns/ Doe	Deer/ Mile	N	Antler/ Antlerless	Deer/ Mile
1966-67	14	14	106	2.79			
1967-68	10	13	100	2.52	16	18	3.92
1968-69	10	13	96	3.48	8	15	3.67
1969-70	8	23	86	4.88	7	14	6.09
1970-71	8	20	72	6.72	7	12	4.43
1971-72	6	24	76	4.78	8	16	10.06
1972-73	8	27	76	7.23	5	17	14.95
1973-74	11	16	85	8.88	6	9	9.62
1974-75	9	23	87	15.03	9	6	9.54
1975-76	10	25	63	6.32	8	9	8.61
1976-77	10	17	61	6.86	6	3	8.00
1977-78	10	16	41	7.12	8	4	6.55
1978-79	9	11	59	6.61	8	9	5.25
1979-80	9	13	56	4.83	9	8	3.17
1980-81	8	15	69	3.44	6	2	1.84
1981-82	8	10	72	3.93	6	6	2.46
1982-83	19	16	72	2.76	14	5	3.00
1983-84	13	15	54	3.19	13	7	3.86
1984-85	14	11	64	2.71	15	7	2.36
1985-86	15	14	79	3.13	14	5	1.74
1986-87	18	12	61	2.46	14	6	2.19
1987-88	19	14	75	2.56	15	4	2.45
1988-89	17	15	61	2.43	--	--	

APPENDIX D. Age structure of Crab Orchard NWR deer harvests, 1973-1988.

	Primary Age Ratio[1]			Proportion Yearlings		Mean Age		
Year	Male	Female	All	Male	Female	Male	Female	All
1973	0.300	0.335	0.314	0.366	0.326	2.21	2.25	2.23
1974	0.352	0.351	0.352	0.415	0.356	1.98	2.00	1.99
1975	0.337	0.401	0.363	0.482	0.285	1.81	2.11	1.93
1976	0.407	0.419	0.412	0.578	0.419	1.65	1.87	1.73
1977	0.255	0.364	0.297	0.566	0.353	1.86	2.02	1.92
1978	0.454	0.342	0.400	0.505	0.233	1.68	2.39	2.01
1979	0.416	0.389	0.402	0.687	0.304	1.55	2.39	1.99
1980	0.447	0.455	0.451	0.634	0.293	1.62	2.23	1.99
1981	0.546	0.389	0.464	0.778	0.352	1.35	2.14	1.74
1982	0.590	0.484	0.537	0.756	0.400	1.31	1.93	1.61
1983	0.423	0.433	0.427	0.766	0.380	1.50	2.06	1.75
1984	0.429	0.366	0.397	0.612	0.355	1.66	2.23	1.94
1985	0.649	0.494	0.571	0.667	0.289	1.48	2.08	1.77
1986	0.505	0.503	0.504	0.782	0.331	1.41	2.02	1.71
1987	0.556	0.531	0.546	0.667	0.290	1.47	2.02	1.68
1988	0.362	0.469	0.402	0.715	0.364	1.58	1.95	1.73

[1] Fawns/all older deer

JOB C. Taxonomic Status of Regional Illinois Deer Herds

Objective: To determine the taxonomic status of regional Illinois deer herds.

INTRODUCTION

Illinois is included within the range of the large northern woodland white-tailed deer (*O. v. borealis*) with another large form, the Kansas white-tailed deer (*O. v. macrourus*) found in the plains states west of the Mississippi River, and a smaller form, the Virginia white-tailed deer (*O. v. virginianus*) found southeast of the Ohio River (Fig. 1). Recent studies have suggested that deer from southern Illinois may be assignable to *virginianus*, based upon their small size yet high productivity and good physical condition (Ritchie 1970; Nelson and Woolf 1985).

Relationships between environmental and genetic components of phenotype in white-tailed deer are not well-understood. Although reproductive, weight, skeletal, and antler characteristics reflect nutritional plane, hence range conditions (Cheatum and Severinghaus 1950, Klein 1964, Ullery 1983), these traits are also under genetic control (Ramsey et al. 1979; Smith et al. 1983). It seems that environment and genetics play an intricate role in determining size in white-tailed deer. Smith et al. (1984:121) have suggested that "differences among white-tail populations throughout the species' range may have genetic constraints, whereby the races or subspecies are restricted within various physiological/morphological 'amplitudes'".

Objectives were to: 1) examine relationships between deer weight by sex/age class and a number of environmental parameters which are thought to

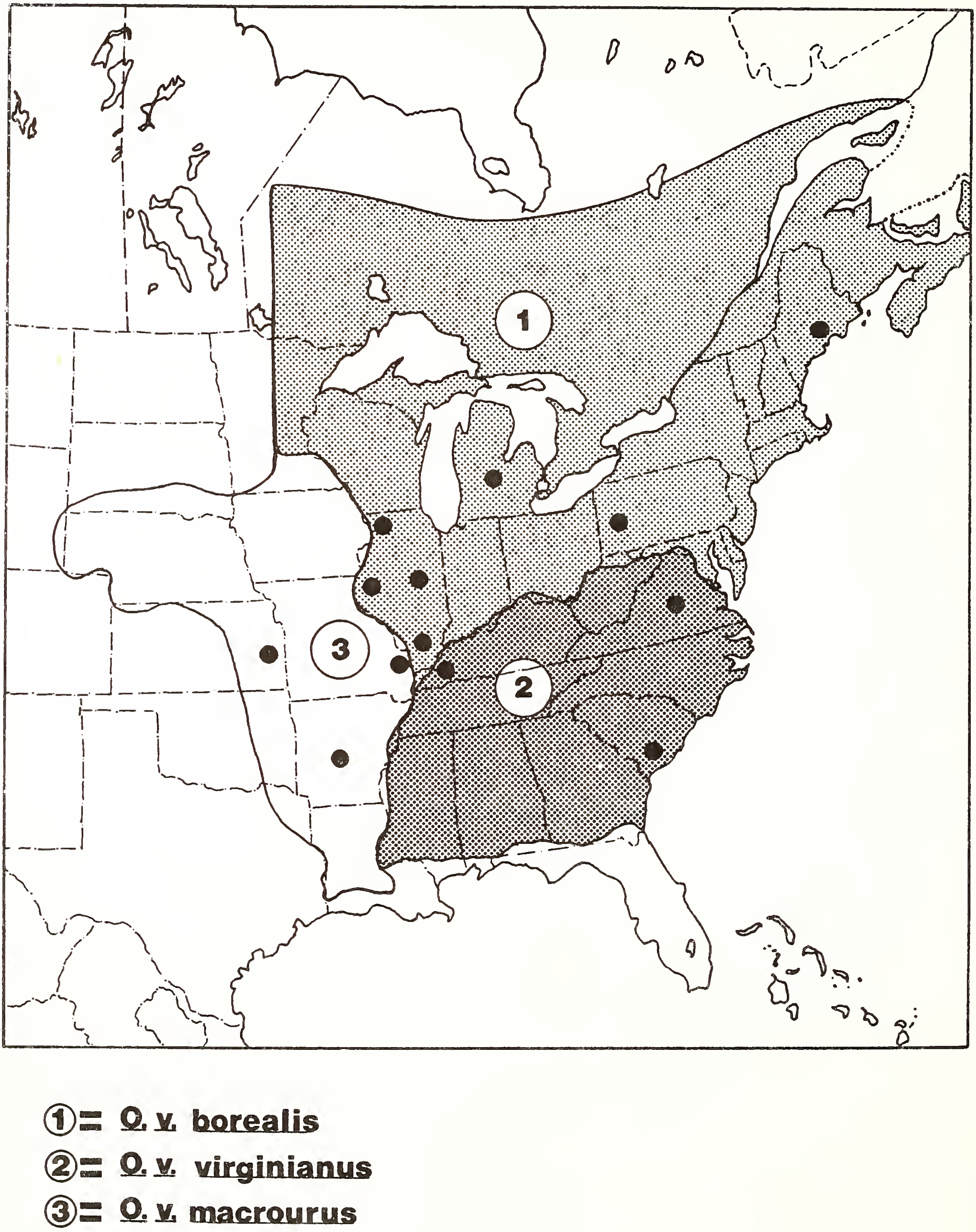

Fig. 1. Current distribution of white-tailed deer subspecies inhabiting the eastern and midwestern United States. Dots represent proposed sampling localities.

influence weight in white-tailed deer; and 2) test the hypothesis that deer from southern Illinois are morphologically distinct from deer inhabiting other regions of the state.

METHODS

Relationships Between Weight and Environmental Factors

A canonical correlation analysis was performed between deer weights by age and sex class and a set of environmental variables with the use of the CANCORR procedure of SAS (SAS Institute, Inc. 1985). Dependent and independent variables are listed in Table 1, along with abbreviations and acronyms used in text. Eviscerated weights were collected at hunter check stations throughout Illinois. Seventy-nine counties and the following years were represented: 1969-72, 1979, 1982-1985. Deer were aged, sexed, and weighed by check station personnel.

Testing for normality revealed slight to moderate skewness for all variables except LAT and HUNTER. Transforming variables increased skewness; original variables were used in the analysis. PAST was dropped from the analysis due to extreme skewness.

Analysis of Skeletal Characters

A multivariate analysis of variance was performed on a series of 20 cranial measurements taken from female white-tailed deer skulls collected in Illinois. Region of collection was the independent variable. In addition, a discriminant function analysis was performed using these 20 cranial

Table 1. List of variables used in canonical correlation.

Dependent	
MF	male fawn
MY	male yearling
MA	male adult
FF	female fawn
FY	female yearling
FA	female adult
Independent	
LAT	latitude
SOIL	soil fertility
CROP	% county in cropland
FOR	% county in forest
GROW	length of growing season
SNOW	annual snowfall
JTEMP	mean January temperature
HUNTER	hunter success

measurements as predictors of membership in 3 groups. Groups were 3 geographic regions of Illinois (Fig. 2). A second MANOVA was performed on a series of 6 external body measurements taken from whole specimens. Again, region of collection was the independent variable. A discriminant function analysis was performed using these external measurements as predictors of group membership. Initial collections of crania and external body measurements from hunter-harvested adult female white-tailed deer have included 3 regions of Illinois (Fig. 2). These regions represent high-kill areas oriented along a latitudinal gradient. Adult females were chosen to reduce age-related variation and to remove secondary-sexual variation.

Specimens were aged according to tooth eruption and wear (Severinghaus 1949). Cleaned and dried crania and rami were measured with a Helios dial micrometer and Dunlap measuring board. A series of 20 measurements were taken on each skull; a series of 6 external measurements were taken from whole specimens (Ann. Fed. Aid Performance Rept., W-63-R(SI)-29, Study IV, 1987).

Results of evaluations of normality, outliers, and homogeneity of variance-covariance matrices were satisfactory. Data were analyzed using the GLM procedure of SAS (SAS Institute Inc. 1985) and the DISCRIMINANT procedure of SPSSX (SPSS, Inc. 1986).

RESULTS AND DISCUSSION

Relationships Between Weight and Environmental Factors

Chi-square tests were significant with all the canonical correlations included ($X^2(42)=3.75$, $\underline{P}= 0.0001$), and with the first canonical correlation removed ($X^2(30)=1.57$, $\underline{P}= 0.03$). With the first two canonical correlations removed, Chi-square tests were not statistically significant ($X^2(20)=1.26$, $\underline{P}=$

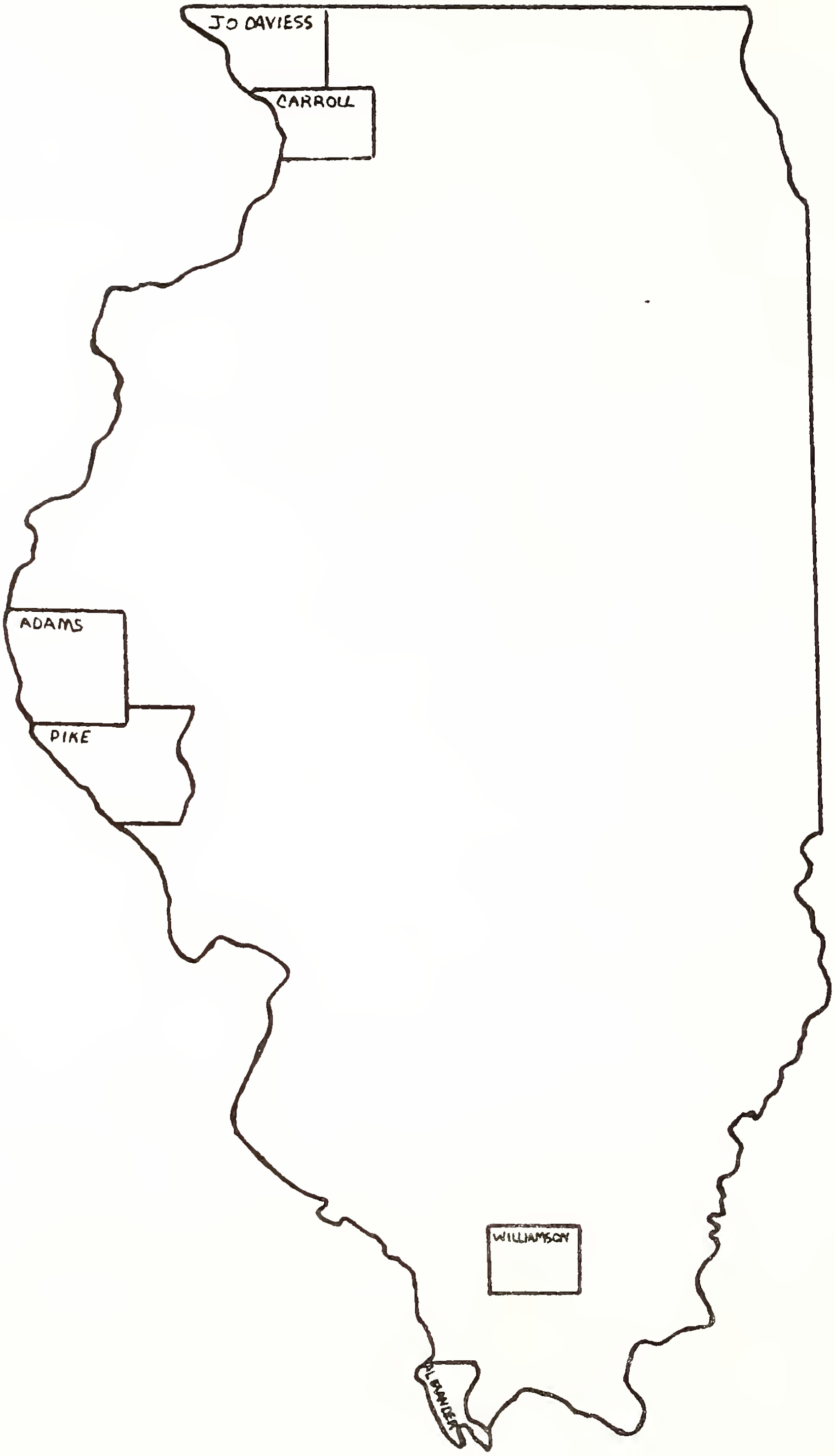

Fig. 2. Specimen collection localities. Regions are northwestern (Jo Daviess and Carroll cos.), westcentral (Adams and Pike cos.), and southern (Alexander and Williamson cos.) Illinois.

0.21). Subsequently, only the first two pairs of canonical variates were interpreted.

The first canonical correlation was .85 (72% of variance); the second was .51 (26% of variance) (Table 2). Total percent of variance and total redundancy indicated that the canonical analysis was more efficient for the first set of variables. Although the second canonical correlation was significant, percent of variance and redundancy indicated that the interpretation of the second pair of canonical variates was marginal at best.

All age/sex classes were highly loaded on the first canonical variate (Table 2). All environmental variables were also highly loaded on the first canonical variate. Taken as a pair, the first canonical variates indicated that greater weights, regardless of age or sex, correspond with increasing latitude, greater soil fertility, higher percentage of county in cropland, lower percentage of county in forest, lower mean January temperature, increasing snow depth, and greater hunter success.

With a cutoff of 0.3 for interpretation, the second pair of canonical variates suggested that lower weight in adult females was associated with lower soil fertility, lower percentage of county in cropland, greater percentage of county in forest, greater snow depths, and greater hunter success. As previously mentioned, interpretation of the second pair of canonical variates is marginal.

All age/sex classes responded in some manner to land-use practices. This relationship between land-use and weight is likely due to range quality. White-tailed deer inhabiting the midwest oak/hickory forest region may have difficulty meeting nutritional requirements (Torgerson and Porath 1984). Conversely, agricultural crops provide a dependable, high-quality food

Table 2. Correlations, standardized canonical coefficients, percents of variance, and redundancies between deer weight and environmental variables and their canonical variates.

	First Canonical Variate		Second Canonical Variate		
	Correlation	Coefficient	Correlation	Coefficient	
Weight - Age/Sex					
MF	.91	.08	-.27	-1.21	
MY	.75	-.11	-.04	- .02	
MA	.72	-.34	-.23	- .32	
FF	.97	.78	-.09	1.85	
FY	.88	.38	.17	1.28	
FA	.92	.17	-.32	-1.71	
Percent of Variance	75.0		5.0		Total= .80
Redundancy	.54		.01		Total= .55
Environmental Variables					
LAT	.87	.34	.22	2.52	
SOIL	.72	-.21	-.37	- .53	
CROP	.70	.12	-.44	.26	
FOR	-.75	-.34	.46	.94	
JTEMP	-.87	-.97	-.17	2.21	
SNOW	.72	-.63	.31	.60	
HUNTER	.51	.27	.33	.43	
Percent of Variance	55.0		12.0		Total= .67
Redundancy	.40		.03		Total= .43
Canonical Correlation	.85		.51		

resource (Gladfelter 1984). Similarly, areas of greater soil fertility undoubtedly provide a higher nutritional plane conducive to increased growth.

Results suggested that weight is related to latitude, mean January temperature, and annual snowfall in a way consistent with Bergmann's Rule. According to this biological rule, warm-blooded animals from colder regions should be larger than their counterparts from warmer climes. Larger animals have a smaller surface area/volume ratio, and should therefore be more efficient at conserving heat. In Illinois, increasing latitude is characterized by colder winter temperatures, increased annual snowfall, and heavier deer.

Hunter success was used as a measure of deer density. If higher hunter success reflects higher densities, a negative relationship between weight and hunter success might be expected. However, if high-kill counties represent optimal deer range and populations have not reached carrying-capacity, a positive relationship between weight and hunter success might be expected. The ever-increasing success rate enjoyed by Illinois hunters in many counties and the above results seem to support this hypothesis.

Analysis of Skeletal Characters

Cranial.--Results of MANOVA testing revealed a significant difference between the 3 geographic regions on the combined dependent variables (Wilks' criterion, F(40, 216)= 3.89, $P<0.0001$). A close relationship existed between geographic region and the combined dependent variables (Pillai's Trace= .81).

ANOVA and multiple-range testing revealed that 14 of 20 cranial characters examined exhibited some degree of geographic variation (Table 3). CRANHT, PALATWID, POSTPAL, INTER, ROSTRAL, and ZYGOMA did not vary significantly between regions whereas NASALEN and PALATLEN varied along a cline, with a progressive increase in size from southern to northern Illinois.

Table 3. Results of ANOVA comparing 20 cranial characters in *Odocoileus virginianus* from three regions of Illinois. Like superscripts denote means not different ($p>0.05$) by Duncan multiple range testing. Data are mean S.D. and (range). Measurements are in millimeters.

Character	NW Illinois (n=36)	WC Illinois (n=56)	S Illinois (n=38)	F-Ratio
GREATLEN	283.1 7.8^{a} (267.0-301.0)	279.5 8.4^{a} (258.0-295.0)	268.4 10.7 (248.0-291.0)	26.0***
CONDYLO	263.1 7.3^{a} (260.0-290.0)	271.1 9.2^{a} (252.0-290.0)	259.1 10.2 (242.0-281.0)	24.2***
NASALEN	96.5 5.7 (84.5-111.6)	94.9 4.8 (86.0-104.3)	87.4 6.0 (76.8-99.9)	28.7***
NASALWID	18.5 1.6 (15.2-21.6)	17.1 2.0^{a} (13.2-20.5)	17.5 2.0^{a} (13.9-21.7)	5.6***
INTER	60.5 2.3 (56.5-64.5)	61.7 3.2 (53.4-67.3)	59.3 2.7 (52.8-66.0)	2.8
ZYGOMA	109.2 3.5 (102.0-117.0)	110.0 3.2 (103.0-119.0)	107.9 4.3 (100.0-116.0)	1.5
PALATLEN	181.2 6.3 (168.0-195.0)	178.0 6.2 (164.0-192.0)	168.6 7.8 (154.0-186.0)	31.0***
PALATWID	26.8 1.6 (23.5-30.0)	27.0 1.4 (23.8-29.8)	26.5 1.6 (23.1-29.9)	0.2
M2M2	74.8 2.1^{a} (70.2-81.3)	75.0 2.5^{a} (69.7-80.0)	72.7 2.8 (66.2-79.9)	8.5***
UPM2M3	79.0 2.7^{a} (73.1-83.7)	78.8 3.7^{a} (71.7-85.9)	74.9 3.3 (65.2-80.6)	12.6***
LPM2M3	88.1 2.8^{a} (83.6-94.4)	88.0 4.1^{a} (79.9-96.6)	83.5 3.7 (73.6-90.3)	16.1***
DIASTEMA	72.8 3.5^{a} (65.3-81.5)	71.6 4.6^{a} (62.6-79.2)	68.1 4.8 (58.6-79.6)	11.4***
INCISIVE	38.5 3.7^{a} (31.6-46.7)	38.0 2.9^{a} (33.5-46.1)	36.0 3.3 (29.2-42.8)	4.0*
CRANBD	74.1 2.5^{a} (67.9-79.7)	74.7 2.1^{a} (70.0-78.6)	72.9 2.4 (67.8-81.4)	4.0*

Table 3. Continued.

Character	NW Illinois (n=36)	WC Illinois (n=56)	S Illinois (n=38)	F-Ratio
CRANHT	68.3 2.0 (63.7-71.9)	68.8 3.0 (63.9-79.5)	68.3 2.4 (62.5-72.7)	0.8
POSTPAL	75.5 3.9 (66.2-84.5)	76.1 4.0 (70.8-86.2)	75.8 3.7 (68.3-83.8)	0.1
CONDYLAR	49.2 1.8[a] (45.8-52.5)	49.7 1.8[a] (45.1-53.5)	46.8 2.4 (42.0-52.0)	19.1***
ROSTRAL	39.9 2.4 (35.4-44.2)	39.6 2.7 (33.4-45.5)	38.6 2.2 (34.6-44.2)	2.5
MANDLEN	221.1 6.3[a] (208.0-239.0)	220.0 7.6[a] (205.0-234.0)	211.1 8.0 (196.0-225.0)	20.3***
MANDHT	108.4 4.9 (98.0-120.0)	104.7 5.2[a] (95.0-118.0)	104.4 5.6[a] (94.0-114.0)	6.5**

*= $p \leq 0.05$, **= $p<0.01$, ***= $p<0.001$

Does from northwestern Illinois were significantly larger than females from westcentral Illinois for only four characters (MANDHT, NASALWID, NASALEN, and PALATLEN); means for the remaining 16 characters did not differ between the two regions. Skulls from westcentral Illinois were significantly larger for 12 of 14 geographically-variable characters, when compared with specimens from southern Illinois. Deer from northwestern Illinois were larger than animals from southern Illinois for all 14 characters exhibiting some degree of geographic variation.

Two discriminant functions were calculated, with a combined $X^2(40)=$ 11.36, $P<0.0001$. After removal of the first function, the second Chi-square test was not significant ($X^2(19)= 30.05$, $P>0.05$). The first discriminant function accounted for 78% of the between-group variability. This function effectively separated southern Illinois specimens from those collected in northwestern and westcentral Illinois (Fig. 3).

The loading matrix of correlations between predictors and the first discriminant function revealed 7 variables with loadings in excess of the .45 cutoff for interpretation (Table 4). The primary distinguishing variable was PALATLEN. GREATLEN, NASALEN, and CONDYLAR were also highly loaded. MANDLEN, LPM2M3, and CONDYLAR were moderately loaded. Six of these predictors are length measurements; CONDYLAR is a width measurement. Specimens from westcentral Illinois averaged slightly smaller than those from northwestern Illinois for all 7 distinguishing variables. Specimens from southern Illinois averaged smaller than those from westcentral Illinois for 6 of 7 variables (LPM2M3 excepted).

The first 5 characters listed in Table 4 were highly positively intercorrelated (r = .56-.93). Correlations between both LPM2M3 and CONDYLAR

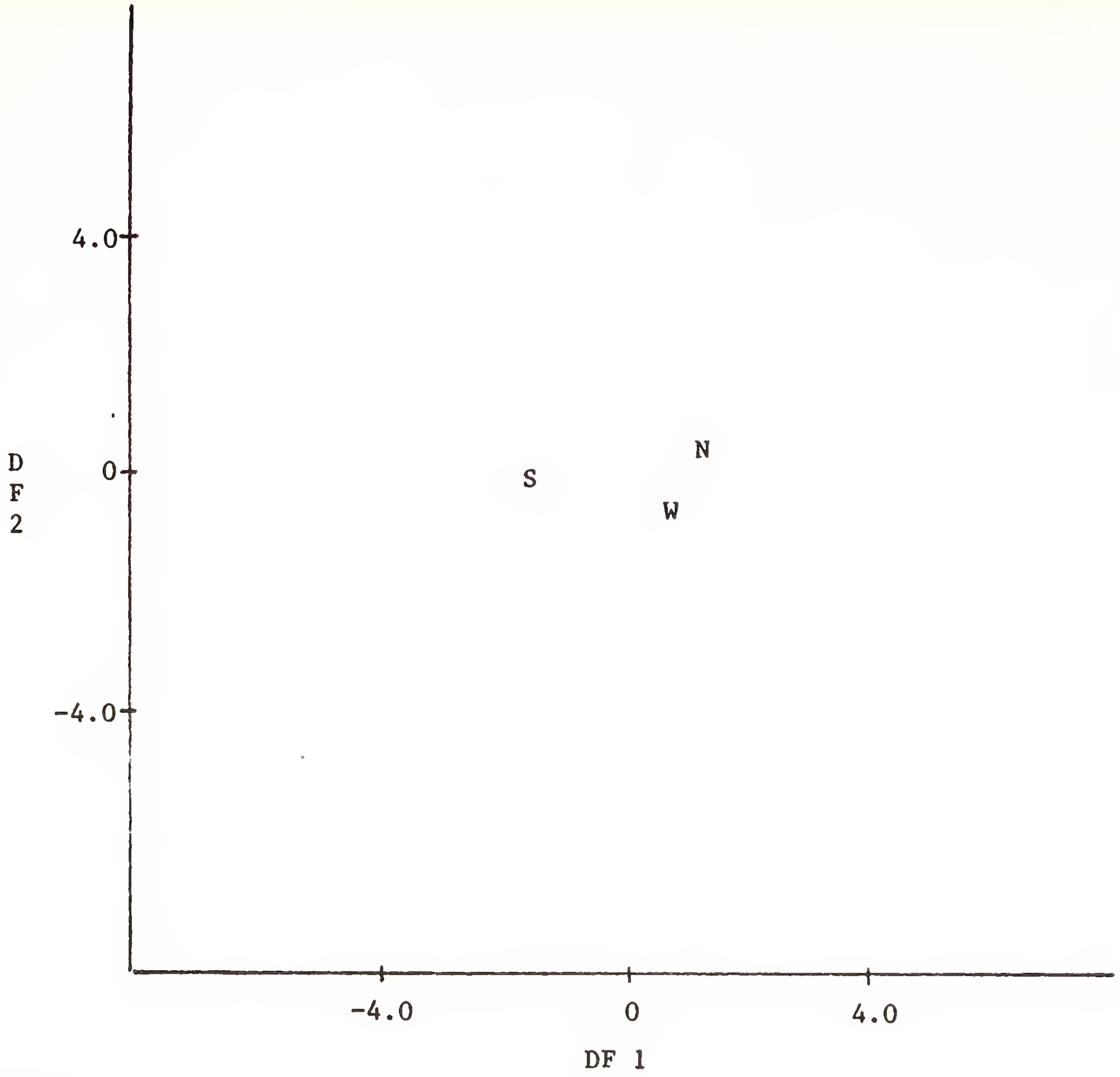

Fig. 3. Plot of three group centroids on two discriminant functions derived from 20 cranial measurements. Groups are southern (S), westcentral (W), and northern (N) Illinois.

Table 4. Results of discriminant function analysis of cranial characters of adult, female white-tailed deer from Illinois.

Predictor Variable	Correlation of Predictors with First Function	Univariate F(2, 109)
PALATLEN	0.66	30.2
GREATLEN	0.62	26.6
NASALEN	0.62	26.7
CONDYLO	0.60	24.3
MANDLEN	0.52	18.4
LPM2M3	0.48	18.0
CONDYLAR	0.46	14.5
Canonical R	0.74	
Eigenvalue	1.24	

and the other variables were low to moderate (r = .15-.41). All correlations between contributing variables were significant.

Of the total sample of 112 skulls, 84 (75%) were classified correctly. Twenty-two of the cases were withheld from calculations during a cross-validation run. Of the 90 cases used in calculating classification functions, 76% were correctly classified. Of those skulls collected in northwestern Illinois, 89% were classed as Group 1 (nw IL) or Group 2 (wc IL). Of those collected in westcentral Illinois, 92% were classed as Group 1 or Group 2. Seventy-nine percent of southern Illinois specimens were correctly classified. A greater number of Group 3 (s IL) specimens were classed as Group 2 (13%) than Group 1 (8%).

External.--There was a significant difference between regions on the 6 dependent variables (Wilks' criterion, $F(12, 138)= 12.83$, $P<0.0001$). There was a close relationship between region and the combined dependent variables (Pillai's Trace= .86).

Results of ANOVA and multiple-range testing revealed a pattern congruent with that observed for skull measurements (Table 5). Four of 6 external characters examined varied geographically. EAR and METATARS did not vary significantly between regions. Deer from northwestern and westcentral Illinois did not vary significantly in size. Animals from westcentral Illinois were significantly larger than those from southern Illinois for all four characters exhibiting geographic variation. Does from northwestern and southern Illinois did not differ significantly for TAIL.

Two discriminant functions were calculated, with a combined $X^2(12)= 107.2$, $P<0.0001$. With the first function removed, the second X^2 test was not significant ($X^2(5)= 8.5$, $P>0.12$). The first discriminant function accounted for 96% of the between-group variability. This function effectively separates

Table 5. ANOVA for six external characters in adult, female white-tailed deer from Illinois. Like superscripts denote means not different by Duncan multiple range testing. Data are mean (S.D.). Measurements are in millimeters.

Character	Northwestern Illinois (n=21)	Westcentral Illinois (n=27)	Southern Illinois (n=29)	F-Ratio
TOTAL	1719.7 (60.1)^{a}	1730.1 (67.6)^{a}	1609.0 (80.0)	25.0***
TAIL	226.0 (22.5)^{a,b}	240.3 (23.3)^{a}	223.0 (30.0)^{b}	3.1*
FOOT	483.8 (13.0)^{a}	480.0 (15.8)^{a}	430.7 (16.5)	106.4***
EAR	160.5 (6.3)	157.1 (10.5)	154.8 (7.5)	3.0
METATARS	28.0 (4.8)	25.4 (5.4)	26.2 (4.1)	1.2
HGTSHLDR	955.5 (45.3)^{a}	963.6 (34.7)^{a}	894.0 (41.0)	25.4***

*= $P \leq 0.05$; **= $P < 0.01$; ***= $P < 0.001$

southern Illinois specimens from those collected in northwestern and westcentral Illinois (Fig. 4).

The loading matrix of correlations between predictor variables and the first function revealed 3 variables with loadings in excess of the .45 cutoff for interpretation (Table 6). The primary distinguishing variable was FOOT. HGTSHLDR and TOTAL were moderately loaded. Specimens from westcentral Illinois averaged larger than those from northwestern Illinois for TOTAL and HGTSHLDR, but smaller for FOOT. Specimens from southern Illinois averaged considerably smaller than specimens from westcentral and northwestern Illinois for all 3 distinguishing variables. These variables were moderately positively correlated (r= .35-.48).

Of the total sample of 77 cases, 65 (84%) were correctly classified. Twenty-four (31%) of the cases were withheld during a cross-validation run. Of these, 79% were correctly classified. All of the specimens from northwestern Illinois were classed as Group 1 (nw IL) or Group 2 (wc IL). Of those from westcentral Illinois, 96% were classed as Group 1 or Group 2. Ninety-seven percent of the southern Illinois specimens were correctly classified. One specimen (3%) from southern Illinois was misclassified as Group 1.

These results support the hypothesis that deer from southern Illinois are morphologically distinct. It is recognized that the regions sampled represent a small portion of Illinois, however, these areas are representative of the range of climatological conditions deer are exposed to, at least latitudinally. Sample sizes are being increased and collections from other regions of the state are being planned. In addition, reference samples from other areas within the range of borealis, microurus, and virginianus are being added to the data set (Table 7).

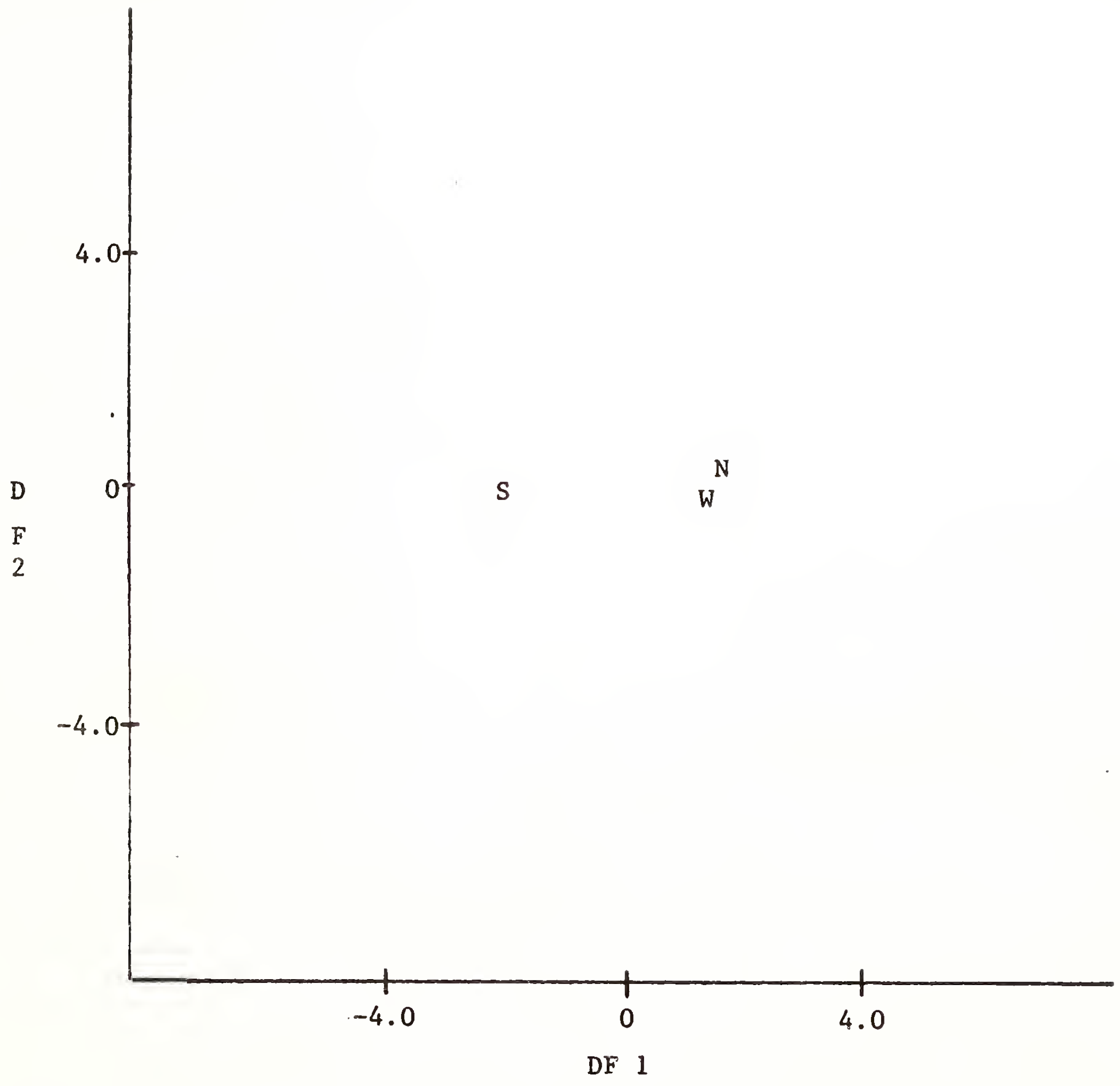

Fig. 4. Plot of three group centroids on two discriminant functions derived from six external body measurements. Groups are southern (S), westcentral (W), and northern (N) Illinois.

Table 6. Results of discriminant function analysis of external body characters of adult, female white-tailed deer from Illinois.

Predictor Variables	Correlations of Predictors with First Function	Univariate F(2, 74)
FOOT	0.98	106.4
HGTSHLDR	0.47	25.4
TOTAL	0.47	24.9
Canonical R	0.87	
Eigenvalues	2.97	

Table 7. Locations of white-tailed deer skulls collected 1986-88.

	Sample Size			
Region	1986	1987	1988	Total
Arkansas	--	10	12	22
Kansas	--	--	25	25
Kentucky	--	--	15	15
Maine	--	--	17	17
Minnesota	24	10	--	34
Missouri	--	27	--	27
Pennsylvania	10	7	10*	27
South Carolina	--	--	20	20
northern Illinois	37	--	27	64
eastcentral Illinois	--	--	15	15
westcentral Illinois	--	70	7	77
southern Illinois	27	43	--	70
Totals	98	167	148	413

* borrowed museum specimens

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Job D. Temporal Variation in Condition Indices

Objective: To determine causes of annual variation in condition indices and their suitability for monitoring herd status.

INTRODUCTION

Following is an abstract summarizing findings for this job and recommendations for application of findings to deer management in Illinois. A thesis is appended to this report in lieu of a Job Completion report.

ABSTRACT

Data needed to calculate values for 36 physical condition indices and index variations were collected from 103 adult (2 years and older) female white-tailed deer (*Odocoileus virginianus*) in southern Illinois. Indices were evaluated on their ability to reflect expected inter- and intraseasonal condition trends and to predict depot fat store levels ($P < 0.10$). Practical aspects of index use and selection were also discussed.

Only 1 index, eviscerated weight (EW), was able to make condition distinctions between paired groups in both inter- and intraseasonal comparisons. However, when indices were placed into 2 subgroups, (1) those effective in detecting interseasonal condition changes within a single herd and, (2) those effective in making intraseasonal comparisons of spatially separate herds, many more indices were deemed useful in their respective categories. EW, percent femur marrow fat, chest girth (CG), serum

cholesterol, average kidney fat index, percent mandible marrow fat (MMF), and the body weight estimation ratios were all significant predictors of depot fat levels and were capable of tracking interseasonal condition trends within a single herd. EW and CG were correlated with fat depot levels and could identify condition differences between spatially separate herds within a single season.

Age factors affected eye lens weight (LENSWGT), MMF, total serum protein, and relative adrenal weights. Abomasal parasite counts were the most time-consuming of indices, and the blood parameters were the most costly.

RECOMMENDATIONS

Management implications for the 36 indices and index variations examined in this study were developed using the criteria previously outlined. Indices were "recommended for use" only if they were (A) capable of making statistically significant ($P \leq 0.10$) condition classifications and (B) correlated to two or more depot fat store levels at a statistically significant ($P \leq 0.10$) level. Indices which consistently suggested the expected condition relationships, but did not indicate statistically significant differences in all cases, were "recommended for further investigation." A few indices (APC, LENSWGT, FHFR, and FL) required information generally not available at deer check stations and/or were significantly affected by age factors; in these cases conclusive analyses were precluded. Following is a summary of findings;

1. Abomasal Parasite Count

Warrants further investigation as an indicator both in inter- and intraseasonal comparisons. Suggested expected condition trends in summer, but lacking data precluded the recommendation of this index. Most time-consuming of the investigated indices. May be of use only in the late summer months due to parasite life cycle. Needed information generally not available at deer check stations.

2. Absolute Adrenal Weight

Not recommended. Inconsistent findings. Body size may affect adrenal weight in addition to physiological stress factors. Needed information generally not available at deer check stations.

3. Bled Weight

Warrants further investigation as an indicator in both inter- and intraseasonal comparisons. Low cost. Needed information generally not available at deer check stations.

4. Bled Weight Estimation Ratio

Recommended for use in tracking interseasonal condition trends within a single herd only. Low cost. Needed information generally not available at deer check stations.

5. Blood Cholesterol

Recommended for use in tracking interseasonal condition trends within a single herd only. Had an inverse relationship to condition. Quite costly to process. High degree (73% compliance) of hunter cooperation in sample collection.

6. Blood Glucose

Not recommended. Inconsistent findings. Values may be affected by stress introduced immediately prior to death. Quite costly to process.

7. Blood Urea Nitrogen

Warrants further investigation. Accurately tracked interseasonal condition trends within a single population at a statistically significant level, but was not a good predictor of depot fat stores. Lacked straightforward interpretation. Quite costly to process. Perhaps would be more useful in conjunction with assays of non-esterified fatty acids. High degree (73% compliance) of hunter cooperation in sample collection.

8. Corpora albicantia

Not recommended. Did not provide a broad scale of condition. Not sensitive to short-term changes in physical status. Needed information generally not available at deer check stations. Information available only in select seasons.

9. Corpora lutea

Not recommended. Did not provide a broad scale of condition. Not sensitive to short-term changes in physical status. Needed information generally not available at deer check stations. Information available only in select seasons.

10. Eviscerated Weight

Recommended for both tracking interseasonal trends within a single herd and making intraseasonal comparisons of separate populations. Only index unquestionably useful in both types of comparisons. Data readily available at deer check stations. Low cost.

11. Eviscerated Weight Estimation Ratio

Recommended for use in tracking interseasonal condition trends within a single herd only. Warrants further investigation in making intraseasonal comparisons between spatially separate herds. Data readily available at deer check stations. Low cost.

12. Eye Lens Weight

Warrants further investigation. Correlation with age precluded conclusive analyses. May be of use in making intraseasonal condition evaluations if age-specific does are used in comparisons. Data obtainable at deer check stations. Low cost. Hunters may be reluctant to provide lenses for analysis due to trophy defacement concerns.

13. Femur/Hind Foot Length Ratio

Warrants further investigation. Resulted in accurate condition classifications where used, but lacking data prevented this index's recommendation. Data obtainable at deer check stations. Low cost. Hunters may be reluctant to provide femurs for analysis due to trophy defacement concerns and/or meat loss.

14. Femur Lenght

Warrants further investigation in making intraseasonal comparisons between spatially separate herds. Resulted in accurate intraseasonal condition classifications where used, but lacking data prevented this index's recommendation. Data obtainable at deer check stations. Low cost. Hunters may be reluctant to provide femurs for analysis due to trophy defacement and/or meat loss concerns

15. Femur Marrow Fat (%)

a. Oven-drying method: Warrants further investigation in making interseasonal comparisons within a single herd. Lacking data precluded conclusive analyses. Data obtainable at deer check stations. Low cost. Quite time-consuming. Hunters may be reluctant to provide femurs for analysis due to trophy defacement and/or meat loss concerns.

b. Visual evaluation method: Not recommended. Very subjective. Useful only in cursory, non-statistical examinations.

16. Fertilization Rate

Not recommended. Did not provide a broad scale of condition. Not sensitive to short-term changes in physical status. Needed information generally not available at deer check stations. Information available only in select seasons.

17. Fetal Counts

Not recommended. Did not provide a broad scale of condition. Not sensitive to short-term changes in physical status. Needed information generally not available at deer check stations. Information available only in select seasons.

18. Girth

Recommended for use in tracking interseasonal condition trends within a single herd. Warrants further investigation in making intraseasonal comparisons between spatially separate herds. Data readily available at deer check stations. Low cost.

19. Girth/Bled Weight Ratio

Not recommended. Inconsistent findings. Information generally not available at deer check stations.

20. Girth/Eviscerated Weight Ratio

Recommended for use in making same-season comparisons between separate populations only. Data readily available at deer check stations. Low cost.

21. Heart Weight

Warrants further investigation in making intraseasonal comparisons of spatially separate herds. Low cost. Needed information generally not available at deer check stations.

22. Hemoglobin

Warrants further investigation. Field collection problems encountered with this index precluded conclusive analyses. Needed information generally not available at deer check stations. Quite costly to process.

23. Hind Foot Length

Warrants further investigation in making intraseasonal comparisons of spatially separate herds. Data readily available at deer check stations. Low cost. Difficulty in standardized measuring may confound results.

24. Hind Foot Length/Bled Weight Ratio

Warrants further investigation as an indicator of interseasonal condition trends within a single herd and of intraseasonal condition disparities between spatially separate herds. Lacking data precluded conclusive analyses. Information generally not available at deer check stations. Low cost.

25. Hind Foot Length/Eviscerated Weight Ratio

Recommended for use in tracking interseasonal condition trends within a single herd. Warrants further investigation in making same-season comparisons of separate populations, but lacking data precluded conclusive analyses. Data readily available at deer check stations. Low cost.

26. Kidney Fat Index (Average)

a. Calculated method: Recommended for use in tracking interseasonal condition trends within a single herd only. Warrants further investigation in making same-season comparisons of separate populations. Low cost. Needed information generally not available at deer check stations. Limited degree (17% compliance) of successful hunter cooperation in sample collection.

b. Visual estimation method: Not recommended. Inconsistent findings. Very subjective. Useful only in cursory, non-statistical examinations.

c. Kidney weight. Recommended for use in making intraseasonal comparisons of spatially separate herds only. Needed information not available at deer check stations. Low cost. Cyclical seasonal weight changes make confound interseasonal condition comparisons within a single herd. Limited degree (17% compliance) of successful hunter cooperation in sample collection.

27. Mandible Marrow Fat (%)

Recommended for use in tracking interseasonal condition trends within a single herd. Warrants further investigation in making intraseasonal comparisons of spatially separate herds. Correlation with age may require that comparisons be made only between age-specific groups. Data obtainable at deer check stations. Low cost. Quite time-consuming. Hunters may be reluctant to provide mandibles for analysis due to trophy defacement concerns.

28. Non-esterified fatty acids

Warrants further investigation. Field problems encountered with this index precluded conclusive analyses. Most costly to process of the investigated indices.

29. Packed-Cell Volume

Warrants further investigation. Field problems encountered with this index precluded conclusive analyses.

30. Relative Adrenal Weight

a. Relative to bled weight: Not recommended. Inconsistent findings. Needed information generally not available at deer check stations.

b. Relative to eviscerated weight: Not recommended. Inconsistent findings. Needed information generally not available at deer check stations.

31. Total Serum Protein

Not recommended. Inconsistent findings. Association with age complicated use of this index. Quite costly to process.

32. Visual Body Fat Evaluation

Not recommended. Inconsistent findings. Very subjective. Useful only in cursory, non-statistical examinations.

33. Y-intercept method

Recommended with reservations. Resulted in accurate condition classification, both in tracking seasonal condition trends within a single herd but the wide range of regression line slopes precluded statistical confirmation of this index's utility. Low cost. Needed information generally not available at deer check stations.

Researchers are reminded that the use of 1 or 2 indices in evaluating a herd's interseasonal change in physical status, or in comparing two herds' status, is not sufficient. To arrive at meaningful conclusions regarding populations' physical condition, we must enlist the simultaneous use of several indices. Only through a consensus of carefully-selected physical condition indices can we make density-related management evaluations with any degree of certainty.

Several factors should be considered when selecting a set of indices for field use: Are you attempting to document changes in physical condition from season-to-season and year-to-year within a single herd, or is the objective to compare spatially separate populations at the same time of year? Will the necessary data be available at deer check stations, or will it require out-of-season collections? What equipment will be required, and is it available/accessible? How costly and time-consuming will the method chosen be? Is the method easily reproduced or is it rather complex? Is the index affected by age differences? Will the index be useful in the season you have chosen for the evaluation? Consider logistics. Choosing the "right" indices can be as much an art as a science.

JOB E. Analyses and Report

Objective: To integrate published data and findings from these studies into management recommendations.

This objective has been met through annual reporting of findings, submission of job final reports, and annual presentations of findings to Illinois Department of Conservation staff. Original data and copies of Quarterly and Annual Fed. Aid Performance Repts. are on file at the Cooperative Wildlife Research Laboratory, Southern Illinois University at Carbondale, Carbondale, IL 62901.